A COMPARISON BETWEEN THE TRIASSIC TRACE FOSSILS OF CHESHIRE AND SOUTH GERMANY

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ABSTRACT. Ten distinct types of invertebrate trace fossils have been collected from the Waterstones and Lower Keuper Marl (= Tarporley Siltstone Formation, Mercia Mudstone Group, U. Scythian-Anisian, L.-M. Triassic, Warrington *et al.* 1980) of north Cheshire. This ichnofauna shows elements assignable to the *Scoyenia* and *Glossifungites-Skolithos* ichnofacies contrasting with the *Scoyenia* ichnofacies assemblage in the underlying aeolian/fluvial 'Keuper' Sandstone (= Helsby Sandstone Formation, Sherwood Sandstone Group, Scythian, L. Triassic—Warrington *et al.* 1980). Within the *Glossifungites* ichnofacies a low-mid intertidal sandflat *Diplocraterion luniforme* association and high intertidal mudflat *Thalassinoides* cf. *suevicus* association are recognized. In terms of behavioural groupings and ichnospecies composition the ichnofauna of the Waterstones compares most closely with that of the Röt (U. Scythian-Anisian) of the south German basin (S. Hessen-Württemberg-Vosges). The Anisian transgression in the Cheshire basin appears to have been both slower and more restricted than in south Germany, where additional *Cruziana* ichnofacies trace fossils and body fossils indicate fully marine conditions preceding the Muschelkalk carbonates.

The trace fossils described from Cheshire and compared with German forms are cf. *Arenicolites* sp., *Diplocraterion luniforme*, *Isopodichnus* sp., *Lingulichnus verticalis*, *Palaeophycus triadica*, *Phycodes curvipalmatum* ichnosp. nov., *Planolites* sp., small stuffed burrows, striated oblique burrows and *Thalassinoides cf. suevicus*.

INVERTEBRATE trace fossils are poorly known from the Triassic of Britain when compared with either vertebrate footprints (Sarjeant 1974) or ichnofaunas of the Germanic facies of the Triassic in the type area (Seilacher 1955, 1963). This reflects lack of suitable exposures rather than the rarity of the traces themselves.

In the Triassic rocks of the Cheshire basin (text-figs. 1 and 2) invertebrate trace fossils have been recorded from three units: the 'Keuper' Sandstone (Helsby Sandstone Formation, Sherwood Sandstone Group; Warrington *et al.* 1980), the Waterstones (Tarporley Siltstone Formation, Mercia Mudstone Group, ibid.), and the Lower Keuper Marl (Mercia Mudstone Group, undifferentiated ibid.). Beasley (1908) reviewed the invertebrate ichnofauna of the 'Keuper' Sandstone of the Wirral and, although his collections are now either lost, or were destroyed by wartime bombing, a brief record of them exists in the Beasley Photograph Collection of the Liverpool Geological Society (Sarjeant 1971). Records of invertebrate trace fossils from the Waterstones and Lower Keuper Marl encountered in the mapping of the Geological Survey (see Ireland, Pollard, Steel, and Thompson 1978, p. 401) were limited to such generalities as 'worm burrows' or 'crustacean marks', until quarrying related to the construction of the Manchester-Cheshire motorway (M56) led to the discovery of a variety of new trace fossils (Ireland *et al.* 1978). Subsequent examination of all available outcrops of the Waterstones (Ireland *et al.* 1978, fig. 1) has yielded ichnofaunas from eight new localities, distributed along 50 km of the strike of these beds in north Cheshire (Table 1).

Recent work on the stratigraphy and palynology of the Trias of the Irish Sea basin (Warrington 1970*a*, 1974*a*; Evans and Wilson 1975; Colter 1978), mainland Britain (Warrington, 1970*a*, 1974*a*, *b*; Warrington *et al.* 1980), and the North Sea basin (Geiger and Hopping 1968; Ziegler 1975; Brennand 1975) now enables fairly accurate correlation and palaeogeographical reconstruction to be made between British and German Triassic sequences (text-fig. 1). The purpose of this paper, therefore, is not only to describe and analyse the trace fossils from Scythian-Anisian rocks of Cheshire but also to compare them with the better known ichnofaunas of south Germany, which the author has recently examined, in order to place them in their environmental and stratigraphical context.

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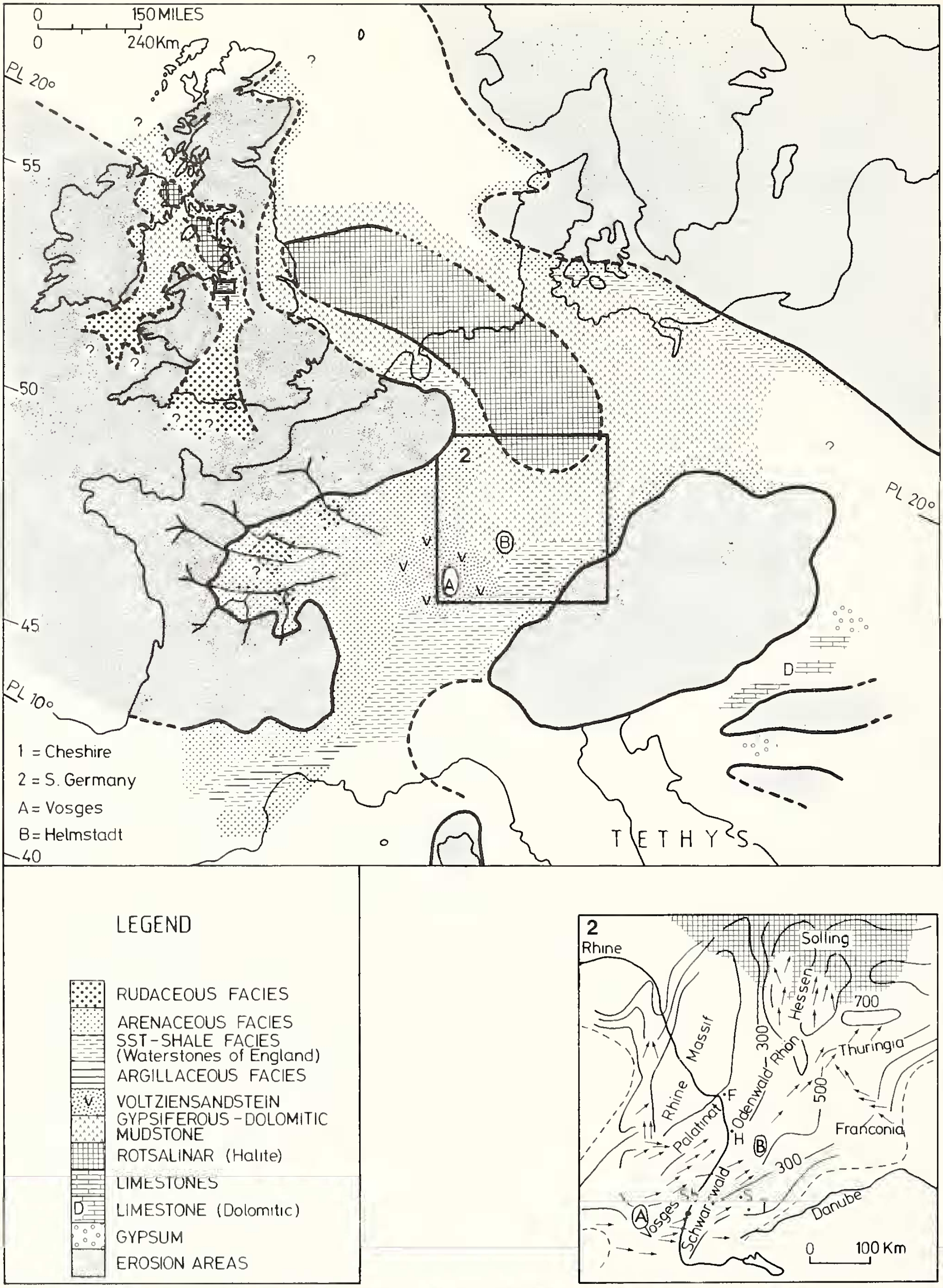
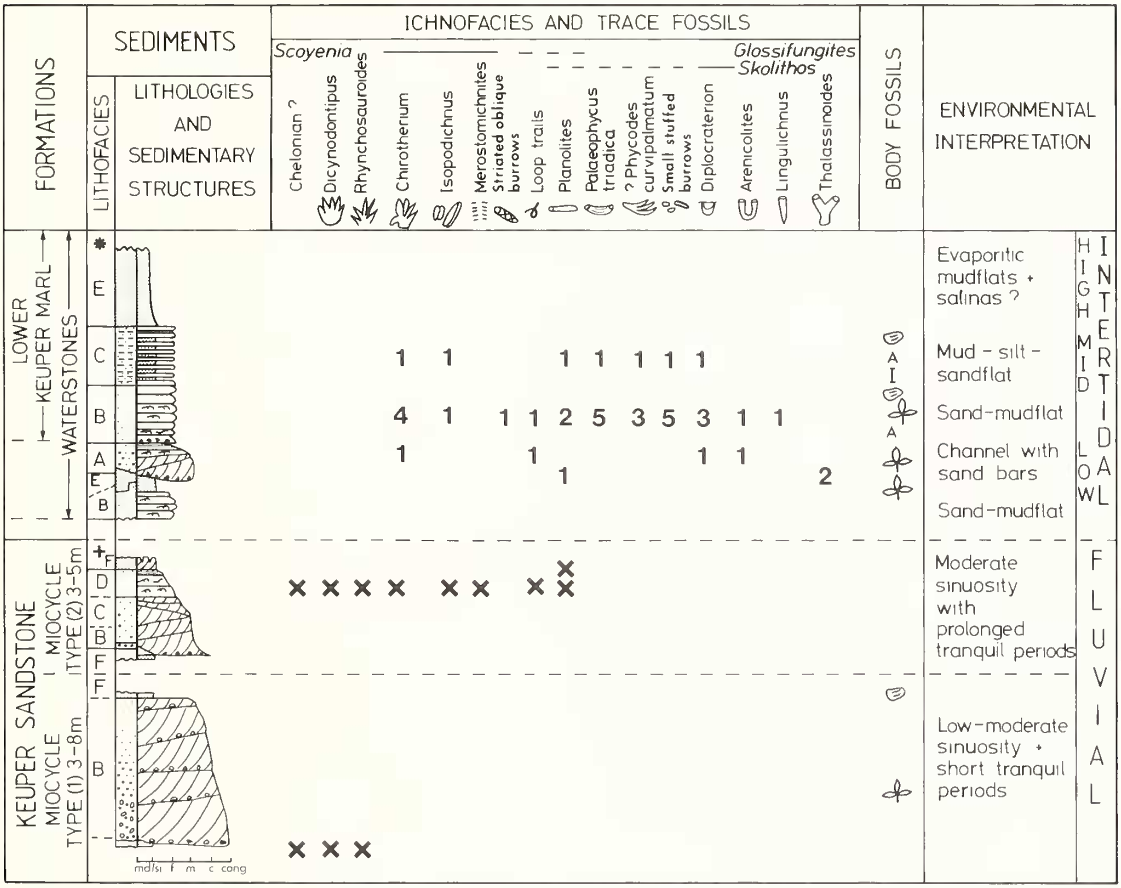


TEXT FIG. 1. Palaeogeographic map of north-west Europe in Röt times (late Scythian–early Anisian) showing location of areas from which ichnofaunas are compared in this paper. Inset map (2) shows Buntsandstein thickness (in m) and areas of Germany mentioned in text. Abbreviations for place-names as in text-fig. 4. (Data from Warrington 1970*b*, 1974*b*; Brennand 1975; Gall *et al.* 1977).

OCCURRENCE OF CHESHIRE TRACE FOSSILS

Stratigraphical position. Although the precise stratigraphical position of the trace-fossil-bearing strata cannot be established at all the new localities recorded, two broad horizons appear to be represented. The lower horizon broadly termed 'Upper Waterstones' (localities 3, 5, and 8) varies from 30 to 80 m above the top of the Frodsham Member of the underlying 'Keuper' Sandstone (= Helsby Sandstone) Formation while the upper horizon (locality 4) > 200 m above the 'Keuper' Sandstone has previously been included in Lower Keuper Marl. In the recent 'Triassic Stratigraphic Report of the Geological Society' (Warrington *et al.* 1980) both these horizons have been included within the newly defined 'Tarporley Siltstone Formation' (Warrington *et al.* 1980, pp. 33–34). Throughout this paper, however, the previous stratigraphic terminology is retained for clarity, although cross-referenced with the new stratigraphical units where appropriate.



TEXT-FIG. 2. Distribution and environmental interpretation of lithofacies, trace fossils, and body fossils of the 'Keuper' Sandstone, Waterstones and Lower Keuper Marl (Scythian–Anisian) in the Cheshire Basin. (*Lithofacies*: *data from Ireland *et al.* 1978, plus data from Thompson 1970*b*. *Sediments*: for key see text-fig. 5. Sediment details shown represent a range and a likely succession of facies in each formation *not* a stratigraphy. For simplicity aeolian sediments, which may interdigitate with the fluvial sediments of the 'Keuper' Sandstone or the Waterstones, are omitted. *Trace fossils*: X—indicates presence; *1*, *3*, etc.—number of localities from which the ichnogenus has been recorded in each lithofacies. *Body fossils*: from other localities. (A—acritarchs, I = insect wing, other symbols as on text-fig. 5).

TABLE 1. Occurrence and relative frequency of trace fossils in the Scythian–Anisian rocks of north Cheshire (see text-fig. 2).

Trace fossils	Localities 1	2	3	4	5	6	7	8	9
cf. *Arenicolites*			C						
Diplocraterion			C/A	A				C	
Isopodichnus			R						
Linguliclmus			R						
Palaeophycus			C	C	C	C		C	
Phycodes			R	R	C			C	C
Planolites		R	R			R	R		
Small stuffed burrows			R	C/A	C/A	R	R	R	
Striated oblique burrows			R						
Thalassinoides	R	R	C						
Chirotherium			C		R	R	R		

(R = rare; C = common; A = abundant)

Locality details:

1. Longley Farm north Quarry (disused), Kelsall (SJ 528699). Waterstones.
2. Finney Hill quarry (disused), Kingsley (SJ 536741). Waterstones.
3. Red Brow Quarry, Daresbury (SJ 571820). U. Waterstones.
4. M56 bridge works, Stretton (SJ 622822). Lower Keuper Marl.
5. M56 cutting, Agden Hall, Broomedge (SJ 714853) U. Waterstones.
6. Boothsbank Lane (Walling slabs), Broomedge (SJ 728848). Waterstones.
7. Warburton Cross (Walling slabs), Lymm. (SJ 699895) Waterstones.
8. M56–M63 cutting, Sharston (SJ 829889). U. Waterstones.
9. Norcliffe Cottage, Styal. (SJ 833832) Waterstones.

Recent correlations of Triassic rocks (Warrington 1974*b*; Colter 1978; Warrington *et al.* 1980) suggest that in a northwards direction, towards the centre of the Northern Irish Sea Basin (or Manx Furness Basin), the trace-fossil-bearing strata pass laterally into a gypsiferous mudstone-halite facies of U. Scythian–Anisian age (text-fig. 1), the Singleton Mudstone Formation of the Blackpool area (Evans and Wilson 1975). Southwards towards the centre of the Cheshire Basin, the Waterstones interdigitates with the Malpas Sandstone Formation (Poole and Whiteman 1966; Colter 1978; Warrington *et al.* 1980) which is probably of aeolian origin (Thompson 1970*b*).

Diversity and distribution. The diversity and relative frequency of trace fossils recorded from Cheshire are shown in Table 1. While the very limited sampling of the Waterstones precludes any general conclusions regarding the geographical distribution of the ichnofauna, it appears that *Chirotherium*, *Palaeophycus triadica*, and the small stuffed burrows are the most widespread elements of the fauna, especially in thin bedded rippled sandstones (lithofacies B—text-fig. 2), where they are often associated with *Diplocraterion luniforme*. Burrows of *Thalassinoides* type are so far known only from the western part of Waterstones outcrop, usually in association with coarser thick-bedded sandstones (lithofacies A—text-fig. 2). Several of the rarer trace fossils (e.g. *Isopodichnus*, *Linguliclmus*, striated oblique burrows) are at present known only from the extensively studied and sampled sequence at Red Brow Quarry (locality 3).

The detailed relationship of trace fossils to stratigraphy and lithofacies could only be studied at Red Brow Quarry, Daresbury (see Ireland *et al.* 1978, pl. 23, tables 1 and 2), and is summarized graphically in text-fig. 5. However, the facies associations, environmental and ichnofacies relationships established there are confirmed by more limited information from the other localities (text-fig. 2). This synthesis forms the basis for the comparison of the Waterstones ichnofauna with those of other horizons and localities in the Germanic facies, which follows (text-figs. 2–5).

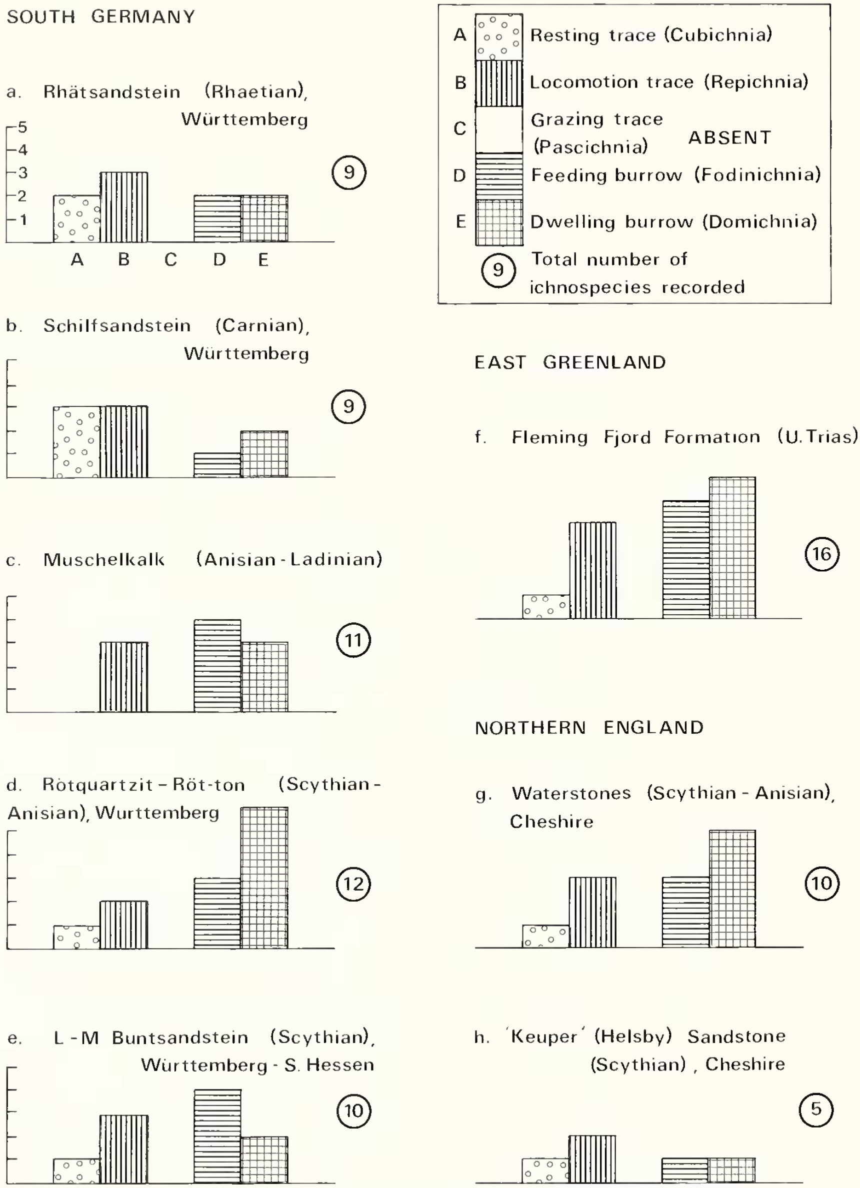
SIGNIFICANCE AND COMPARISON OF THE WATERSTONES ICHNOFAUNA

Ethological groups of trace fossils. Four major behavioural (ethological) groups of trace fossils are present in the Waterstones ichnofauna (text-fig. 3) (Seilacher 1953, 1955). Resting traces are represented by *Isopodichnus* (*Rusophycus* type) and possibly some of the small stuffed burrows, while other specimens of *Isopodichnus* (*Cruziana* type), looped trails, and *Palaeophycus triadica*, together with vertebrate footprints, represent locomotion traces. In common with most ichnocoenoses of the Germanic facies (text-fig. 3), grazing traces are absent, feeding burrows (stuffed burrows, *Planolites* and *Phycodes*) are of limited diversity, and dwelling burrows (*Diplocraterion*, cf. *Arenicolites*, *Lingulichnus*, *Thalassinoides*, and striated oblique burrows) are dominant. Although the total number of trace fossils (ichnospecies) recognized in the Waterstones is similar to that of several formations in the German Trias, the behavioural histogram (text-fig. 3) most closely resembles that of the Röt sequence, an observation which is developed in the more detailed comparison of ichnofaunas below (text-figs. 4 and 5).

Ichnofacies assignment. Ichnofaunas of Triassic red-bed sequences have played an important part in the development of the ichnofacies concept, particularly as applied to non-marine environments (Seilacher 1955, 1963; Bromley and Asgaard 1972, 1979). Seilacher (1963, 1967) established the *Scoyenia* ichnofacies partly on the ichnofaunas and lithofacies of the Schilfsandstein and Middle Buntsandstein of the German Trias (text-figs. 3 and 4), while recently Bromley and Asgaard (1979) and Clemmensen (1978) have recognized distinct trace fossil associations correlating with different freshwater environments within this broad ichnofacies in Upper Triassic sediments from East Greenland (text-fig. 3*f*). It is important, therefore, to examine this aspect of the Waterstones ichnofauna.

The ichnofauna of the Waterstones (text-figs. 2 and 4) contains elements which can be assigned to the *Scoyenia* and the *Glossifungites*–*Skolithos* ichnofacies (Ireland *et al.* 1978, pp. 421–422). There is also a component of looped trails, endichnial and hypichnial burrows (text-fig. 2, centre; text-fig. 4, right; text-fig. 5, column 3) which it is difficult to assign to either ichnofacies and which are best regarded as 'facies-crossing forms' (Seilacher 1964). The apparent *Scoyenia* components (*Chirotherium*, *Isopodichnus*, and striated burrows, text-figs. 2, 4, 5) represent surface traces of either vagile reptiles traversing mudflats or of arthropods living in shallow temporary pools, situations which could have existed on either fluvial floodplains or tidal flats. Although there is some similarity here with the *Rusophycus* ichnocoenosis of Bromley and Asgaard (1979) (desiccated fluvial flood plain), both in trace fossil composition and presence of pre-mudcrack and post-mudcrack burrowing, the detailed sedimentology (Ireland *et al.* 1978), lack of a truly terrestrial trace fossil suite, and absence of true *Scoyenia*, excludes such a detailed comparison. The endichnial dwelling burrows (*Diplocraterion*, cf. *Arenicolites*, *Lingulichnus*, and *Thalassinoides*) suggest an established intertidal infauna, while the 'facies-crossing forms' are essentially surface or near surface locomotion traces or feeding burrows, the ephemeral nature of which is unlikely to reflect the substrate and environmental factors responsible for the major ichnofacies distinctions.

The representation of the *Glossifungites* ichnofacies in the Waterstones ichnofauna is indicated by the forms of the burrows of both *Diplocraterion luniforme* and *Thalassinoides* cf. *suevicus*. When Seilacher (1967) defined this ichnofacies, he stressed the distinctive characters of spreiten-bearing U-burrows as showing only protrusive, distally enlarging forms of *Diplocraterion* (e.g. Pl. 86, fig. 2) or oblique forms of *Rhizocorallium* for which he used the name *Glossifungites* (cf. Seilacher 1967, p. 419, fig. 2 and Pl. 86, figs. 2 and 4). He considered that retrusive parallel-sided (*D. parallelum*) or proximally divergent (*D. habachi*) forms of *Diplocraterion* were diagnostic of *Skolithos* ichnofacies



TEXT-FIG. 3. Comparison of the behavioural (ethological) groups of trace fossils represented in the ichnofaunas of the 'Keuper' (Helsby) Sandstone and Waterstones of Cheshire with those present in other Triassic formations from south Germany and east Greenland. (Data for *a–c*—Seilacher 1955; *f*—Bromley and Asgaard 1979. Other data from author's observations).

(e.g. Rhätsandstein ichnofauna text-figs 3 and 4). Such criteria were supported by later workers (Fürsich 1975, Frey 1975). However, other workers from studies in recent environments (Frey and Mayou 1971; Basan and Frey 1977) have stressed the importance of sparse vertical burrows (e.g. *Arenicolites*, *Lingulichnus*, Table 1, text-fig. 2) and irregular, horizontal branching, unlined arthropod burrows (e.g. *T.* cf. *suevicus*, Pl. 90) in this ichnofacies as contrasting with the abundance of *Skolithos* and vertical *Ophiomorpha* type of arthropod burrows, in the *Skolithos* ichnofacies (Frey 1975).

Two different trace-fossil sediment associations within the *Glossifungites* ichnofacies, which accord with previous environmental interpretations based on sedimentology (Ireland *et al.* 1978), can be recognized in the Cheshire Waterstones. Firstly, the widespread thin-bedded rippled sandstones and siltstones (lithofacies B and C) of inferred mid-intertidal flat origin (text-fig. 2) exhibit bedding-plane communities of *D. luniforme* (Pl. 86, figs. 1 and 5), sometimes showing distal-tube enlargement or obliquity (Pl. 86, figs. 2 and 4), reflect the low-energy or omission-surface environmental expression of this ichnofacies of Seilacher (1967, fig. 3*d*). Secondly, the irregular horizontal burrow networks of *T.* cf. *suevicus* were dug in unbedded blocky mudstones or siltstones (lithofacies E of Ireland *et al.* 1978) of higher intertidal or supratidal origin (text-fig. 2), but were only preserved where such burrow systems were exposed by migrating channels and then infilled by channel bar sandstones (text-figs. 2 and 5; Ireland *et al.* 1978, fig. 7); they parallel the Recent salt-march ichnocoenosis described by Bassan and Frey (1977). The presence of the *Skolithos* ichnofacies in the Waterstones has been recognized only within the channel bar sandstones at locality 3 (text-fig. 5, left) where slightly larger retrusive *Diplocraterion* burrows, deep vertical burrows (cf. *Arenicolites*) and rare *Ophiomorpha*-type oblique variants of *T.* cf. *suevicus* burrows (Pl. 90, figs. 2, 3, and 4) occur.

The apparent overlap of *Scoyenia* and *Glossifungites–Skolithos* ichnofacies present in the Waterstones is entirely consistent, therefore, with the range of sedimentary environments which this formation represents, the gradual transgression of intertidal conditions over both aeolian and fluvial-floodplain facies of the underlying 'Keuper' Sandstone (text-fig. 2 and Ireland *et al.* 1978).

Comparison with ichnofauna of the 'Keuper' Sandstone. The only other ichnofauna from the British Trias which is sufficiently diverse and well known for direct comparison with that described here comes from the 'Keuper' Sandstone (Helsby Sandstone Formation) also in Cheshire (text-figs. 2 and 3). This formation underlies the Waterstones and has been subjected to detailed sedimentological analysis throughout the Cheshire Basin by Thompson (1970*a*, *b*), although trace fossils are mainly known from the Storeton area of the Wirral (Beasley 1908; Thompson 1970*b*; Sarjeant 1974). Recent work by the author on local museum collections and the Beasley Photograph Collection (Sarjeant 1971) has enabled the invertebrate traces to be named and compared with ichnofaunas of the Buntsandstein of Germany (compare text-figs. 2, 3, and 4).

The invertebrate ichnofauna of the 'Keuper' Sandstone (text-fig. 2), characterized by arthropod traces and meniscate burrows ('*Planolites*') in association with fluvial sediments, indicates that this formation belongs to the *Scoyenia* ichnofacies (Seilacher 1963, 1967), although the index form *Scoyenia* has not yet been recorded. The presence of *Isopodichnus* (*Rusophycus* type) and *Merostomichnites* (*Diplichnites*) *triassicus* in the 'Keuper' Sandstone invites comparison with the aquatic suite of the *Rusophycus* ichnocoenosis of the Fleming Fjord Formation of Upper Triassic age in East Greenland (Bromley and Asgaard 1979). Such a comparison is supported by Thompson (1970*b*, pp. 202–203, fig. 8) who pointed out that both vertebrate and invertebrate trace fossils of the 'Keuper' Sandstone are most abundant in thin-bedded rippled and mudcracked fine sandstones (text-fig. 2), which he interpreted as fluvial floodplain top-stratum formed in more prolonged tranquil periods of sediment accumulation by rivers of moderate sinuosity. Furthermore, he interprets such sediments and inferred processes as very similar to those of the dominant arenaceous lithology of the Waterstones (lithofacies B), but lacking evidence of the former evaporitic component, and other features suggestive of an intertidal environment (Thompson 1970*b*, p. 201).

Stage	Group or Formation	Area	Vertebrate footprints	Isopodichnus (Rusophycus)	Isopodichnus (Cruziana)	Merostomichnites (Ichnyspica)	Scoyenia	Cylindricum	Sagittichnus	Diplocraterion luniforme	Diplocraterion parallelum	Arenicolites	Lingulichnus	Pelecypodichnus	Asteriacites	Thalassinoides	Rhizocorallium	Bolonoglossites	Teichichnus	Kouphichnium	Loop trails	Taenidium	Planolites	Palaeophycus	Phycodes	Biformites	Small stuffed burrows
ICHNOFACIES			Scoyenia							Glossifungites - Skolithos						Cruziana				Facies crossing forms							
Rhaet	ko RHAT SST.	Wurttemberg 1		(?)							⊗	⊗		⊗	⊗					⊗					⊗		
Norian	km4 STUBEN SST. 3 KIESEL SST.	Wurttemberg 2	⊗	⊗			?	⊗														⊗	(?)		⊗	⊗	
Carnian	km2 SCHILF SST.	Wurttemberg 3	⊗	⊗	(?)	⊗		⊗	⊗			○		⊗						⊗	⊗	⊗			×		⊗
Ladinian	mo U MUSCHKLK	Wurttemberg 4										△					△⊗	△⊗			△?			△⊗			
Anisian	mu L MUSCHKLK	Wurttemberg 5												○	○	△⊗	○△⊗	△	△						○		
Anisian -Scythian	WATERSTONES	Cheshire	×		×					×		×	×			×					×		×	×	×		×
Anisian	UPPER so BUNT SST (=RÖT)	Kl. Odenwald 6	×	×	×			×		×		×	?			×	×			?			?	×	×		×
		N Vasges 7	⊗	⊗						○			⊗				⊗			⊗		⊗	⊗	⊗			
Scythian	MIDDLE sm BUNT SST	S Hessen 8	⊗	⊗	⊗	⊗	⊗			⊗										⊗	?	⊗	?	⊗	⊗		
		Thuringia 9		○	○			○		○							○						○				○
	LOWER su BUNT SST.	S Hessen 10	○	⊗	⊗	⊗																					
		Thuringia 9	○	○				○									○						○				

LEGEND: × Author's observation ○ In literature (clastics) △ In literature (carbonates)

TEXT-FIG. 4. Comparison of the composition of the ichnofauna of the Waterstones with those of Triassic formations in the south German Basin and its margins. *Key* to literature and collections cited: 1—Rieth 1931, Aepler 1974, T, S, F; 2—Linck 1961, L, T, S, F; 3—Linck 1949, L, T, S, F; 4—Mayer 1957-8, S; 5—Schwarz 1975, T; 6—Gehenn Collection H; 7—Gall 1971, 1973, Sb; 8—Backhaus 1967, T, F, D; 9—Hoppe 1965; 10—Diederich 1967, T, F, D. Collections D = Darmstadt, Techniche Hockschule, Landesmuseum; F = Frankfurt, Senckenberg Museum; H = Heidelberg, Geological Institute; L = Linck private collection; S = Stuttgart, Museum fur Naturkunde; Sb = Strasbourg, Geological Institute; T = Tübingen, Palaeontological Institute.

Comparison with Triassic ichnofaunas of the south German Basin. Text-figs. 3 and 4 show that the ichnofauna of the German Trias is more diverse and better known than that of the British Trias. A greater variety of lithologies and a richer fauna of body fossils, coupled with continued quarrying of much of the sequence for building, industrial and agricultural purposes, enable the ichnofauna to be assessed in terms of modern stratigraphical and sedimentological work. The data recorded on text-fig. 4, derived from both published work and personal observation, come from the Baden-Württemberg and south Hessen areas of Germany—the marginal area of the German Basin most comparable palaeogeographically to the Cheshire Basin (text-fig. 1). Most of the ichnogenera present in the Waterstones are represented in the German Trias and, in terms of ichnofacies again, it appears that non-marine *Scoyenia* and marine *Glossifungites-Skolithos* components together with a number of facies-crossing forms, are present. However, the subtidal marine *Cruziana* ichnofacies is also represented, especially in the Röt and Muschelkalk, reflecting more open marine conditions of the Middle Trias of the German Basin (Schwarz 1975; Gall, Durand and Muller 1977).

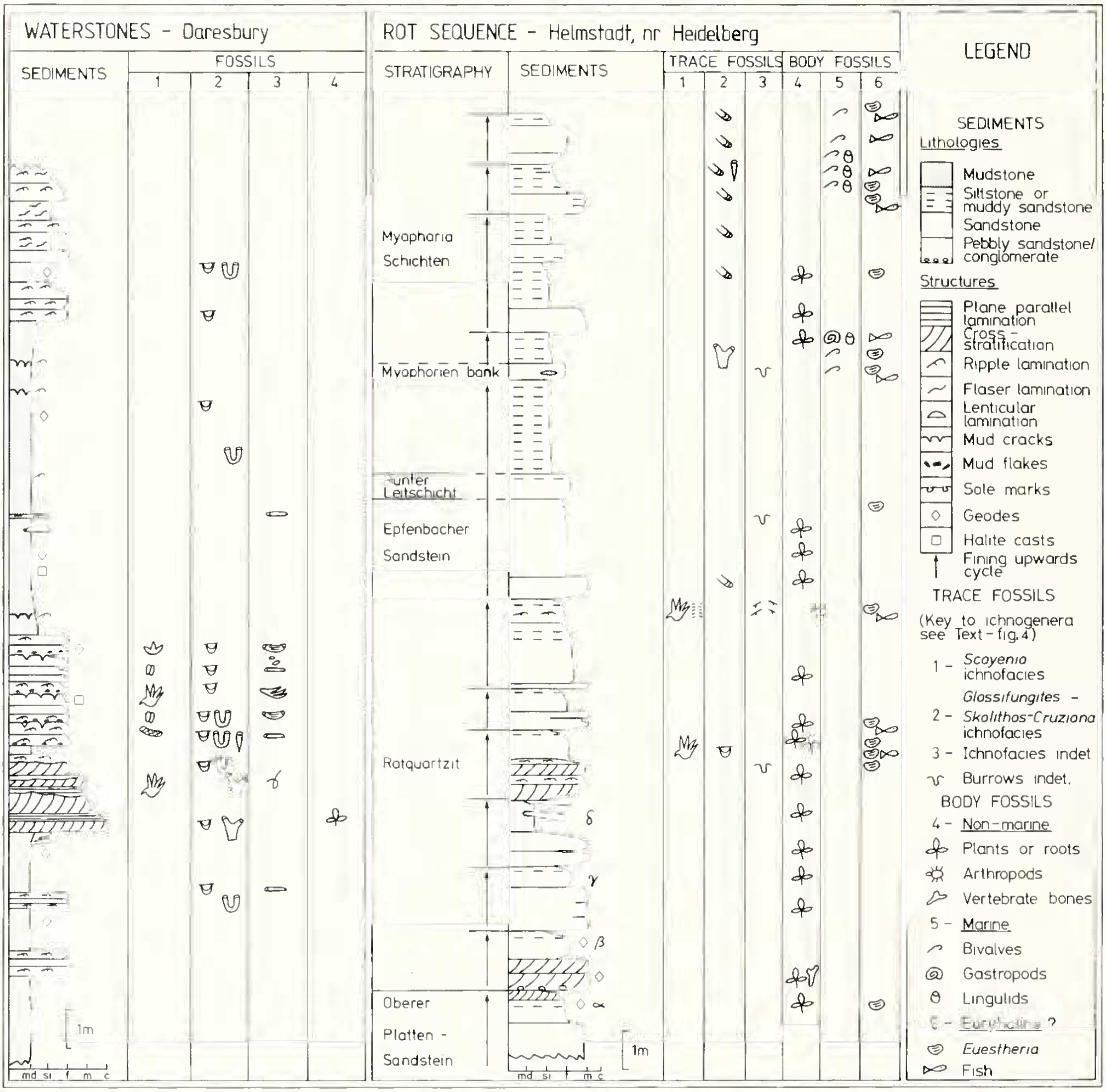
The ichnofauna of the Lower Buntsandstein more closely resembles that of the 'Keuper' Sandstone than that of the Waterstones, as it is dominated by *Isopodichnus* and *Merostomichnites*. Only towards the centre of the German Basin in Thuringia have trace fossils resembling *Rhizocorallium* or even *Helminthoida* been recorded, but even there the sedimentary environment is interpreted as lacustrine rather than marine (Hoppe 1965). *Scoyenia* ichnofacies traces also dominate the Middle Buntsandstein (text-fig. 4; Seilacher 1963) but here the development of the classic 'Folgen' or 'megacycles', the widespread occurrence of *Diplocraterion luniforme*, and the presence of marine bivalve faunas from Hessen northwards (text-fig. 1) (Backhaus 1971) suggest tectonic instability (Backhaus 1974) and possibly marine influence from the north-west (Kozur 1975). The environmental significance of *D. luniforme* has long been controversial (Richter 1926; Schindewolf 1928*b*; Lohmann 1960; Seilacher 1963) and, whilst not by itself regarded as a reliable indicator of intertidal or marine conditions, it appears to represent a distinctive, size-restricted mudflat community probably capable of existing under variable salinity conditions. Once again it is only in the more basin centre situation of Thuringia that *Rhizocorallium* has been recorded.

Undoubtedly it is in the ichnofauna of the Upper Buntsandstein or Röt that the closest comparison to the Waterstones is to be seen, from studies both north of the Vosges (Gall 1971) and south of the Odenwald (Gehenn 1962) (text-figs. 1 and 4). In the lower part of the Upper Buntsandstein (Grès a meules, Rötquartzit) a *Scoyenia* ichnofauna dominates (text-figs. 4 and 5), to be replaced by a *Lingulichnus–Rhizocorallium* ichnofauna associated with marine bivalves as the Röt transgression proceeds. Further to the north these marginal marine strata pass into marine evaporite deposits of the Röt Gips in Nord-Hessen and Thuringia, and into the Röt Salinar in Solling and Nordhannover (Richter-Bernburg 1974; Gall *et al.* 1977) (text-fig. 1). Under the widespread fluvial and lagoonal conditions which preceeded the Röt transgression, body fossils and trace fossils indicate that very diverse vertebrate, arthropod, fish, and plant communities flourished in all areas (Demathieu and Haubold 1972; Gall 1971; Gehenn 1959, 1962; Hoppe 1965), broadly similar to, though far richer than, those known from the time equivalent Bromsgrove Sandstone Formation in Britain (Wills 1910, 1970; Warrington 1976; Warrington *et al.* 1980).

In studies of the sediments and fauna of the Upper Buntsandstein of the Kleinen Odenwald, east of Heidelberg, Gehenn (1962) and Backhaus (1974) have documented in detail the sedimentary rhythms of the Röt quartzite and the transgression of the Röt marine facies. Although detailed facies comparison has not been possible, an examination of the Gehenn Collection in the Geological Institute, University of Heidelberg, has made it possible to compare the vertical distribution of sediments and faunas of a 25 m sequence of the Röt near Heidelberg with that of the Waterstones in Cheshire (text-fig. 5). Body fossils are much more abundant in Klein Odenwald than in Cheshire and, although possible euryhaline faunas like fish and *Euestheria* occur throughout the sequence, a distinct marine transgression is documented by both body and trace fossils. The Rötquartzit shows a *Scoyenia* ichnofauna (*Chirotherium*, *Merostomichnites*, *Kouphichnium*, *Diplocraterion*, and *Planolites*) comparable to Middle Buntsandstein or 'Keuper' Sandstone of Cheshire (compare text-figs. 2, 4, and 5). The marine transgression is shown by the appearance of *Lingulichnus*, *Rhizocorallium*, and even *Thalassinoides suevicus*, associated with marine bivalves including *Myophoria vulgaris* (Anisian age index Kozur 1975), *Lingula*, and marine gastropods—all precursors of Muschelkalk faunas. In the Cheshire sequence there is a virtual absence of body fossils and no clear vertical separation of supposedly non-marine and marginal marine ichnofaunas (see above), although the distinctive burrow *T. suevicus* is identical to the Helmstadt form. At Helmstadt the change from *Scoyenia* to *Cruziana* ichnofacies occurs in the few metres with hardly any representation of intertidal environment (*Skolithos–Glossifungites* ichnofacies), reflecting the rapid southward transgression of the Röt marine facies in this marginal situation (Backhaus 1971). In contrast, at Daresbury the trace-fossil-bearing sequence makes up only 20% or so of the total thickness of the Waterstones there and begins about 80 m above the top of the 'Keuper' Sandstone (*Scoyenia* ichnofacies), reflecting considerable interdigitation of facies and fluctuation of environmental conditions.

The fully marine character of the Muschelkalk of Germany is as much reflected by its ichnofauna as by its body fossils (text-fig. 4). The Lower Muschelkalk ichnofaunas of both the sandy marginal facies (Schwarz 1975) and the carbonate facies (Muller 1956, 1959; Schwarz 1975) belong to *Cruziana* ichnofacies representing littoral–sublittoral depth zones (Schwarz 1975, p. 66). *Thalassinoides* cf. *suevicus* appears to be the only trace fossil common to the Cheshire Waterstones and Lower Muschelkalk of south Germany, the burrow forms from Wellenkalk of Frankonia (Reis 1910, pl. 12) being very similar to those from Cheshire. In the Wellenkalk, however, the burrows occur in largely sub-tidal or intertidal carbonate substrates in common with Jurassic (Fürsich 1974*b*) and Cretaceous (Kennedy 1967) occurrences, and so contrasts with their restriction to intertidal sandstone, siltstone, or calcareous mudstones deduced for the Waterstones (text-fig. 2). The ichnofauna of the Upper Muschelkalk is largely in muddy carbonate facies dominated by *Rhizocorallium–Palaeophycus* type burrows (Mayer 1952, 1958) although some facies-crossing forms and questionable *Arenicolites* on rippled carbonate mudflats (Trusheim 1934; Mayer 1957) show some common elements with the Waterstones.

Trace fossils are poorly known from the regressive marine sequence of the Lower Keuper ('Lettenkeuper') (Brenner 1973), but they reappear with the incoming of sandstones in the Middle



TEXT-FIG. 5. Comparison of the distribution of sediments and fossils of the Waterstones at Daresbury (locality 3) with that of the Röt sequence at Helmstadt, Baden-Württemberg. Data of Röt sequence from Gehenn (1962), Backhaus (1974), and Gehenn Collection, Heidelberg.

Keuper (km 2–4) (Linck 1961, Gwinner 1977). The Schilfsandstein (km 2), representing deltaic conditions advancing southwards from the Baltic area (Wurster 1964), contains trace fossils of *Scoyenia* ichnofacies type (Linck 1949; Seilacher 1955, 1963) associated with the channel ('flutz') facies and restricted marine bivalve faunas (Linck 1968) in interdistributary lagoonal ('normal') facies (Wurster 1964, 1965; Gwinner 1977). The higher Middle Keuper sandstones, Kieselsandstein (km 3) and very thick Stubensandstein (km 4) also possess *Scoyenia* ichnofacies traces (Linck 1961), again suggestive of deltaic or fluviatile origin, but derived from a south-easterly or easterly source area of the Bohemian or Vindelician massifs (Gwinner 1977). These Middle Keuper sandstones appear to have only *Isopodichnus*, loop trails, and some feeding burrows in common with the Waterstones; the over-all ichnofacies more closely approach those of the English 'Keuper' Sandstone or the German Lower and Middle Buntsandstein (text-fig. 4). However, the presence of limulid tracks and rare *Arenicolites* in the Schilfsandstein may suggest some coastal elements. The Upper Keuper (ko) or Rhaetian Rhätsandstein of south Württemberg completes the succession of horizons bearing trace fossils in the German Triassic sequence and represents the appearance of *Skolithos* ichnofacies with an abundant *Arenicolites–Diplocraterion parallelum* association (text-fig. 4) in shoreline and condensed deltaic orthoquartzite sandstones (Seilacher 1967; Aepler 1974).

Conclusions. This review and comparison of the ichnofaunas shows that the trace fossils from the 'Keuper' Sandstone and Waterstones of north Cheshire have both environmental and stratigraphical significance, albeit the latter of a limited kind.

The change of ichnofauna from the 'Keuper' Sandstone to the Waterstones parallels that documenting the Röt transgression on the south-east margin of the German Basin, although the considerably greater stratal thickness, the overlap of non-marine and intertidal ichnofaunas, and the absence of open marine trace fossils suggest a more gradual and limited transgression in the case of Cheshire. The dominance of the Waterstones ichnofaunas by surface-locomotion traces or restricted shallow infauna of intertidal mudflat–sandflat type is consistent with the Anisian transgression in Cheshire never having proceeded beyond the intertidal zone, and with the palaeographical position of north Cheshire at this time, on the southern margin of the Irish Sea basin (text-fig. 1). Recent correlations northwards towards the centre of the Irish sea basin confirm the presence of gypsiferous-halite ('Keuper' facies) contemporaneous with the Muschelkalk facies (Anisian) of east North Sea and German Basins (Warrington 1970, 1974*b*; Brennand 1975).

In terms of stratigraphical significance, while the vertebrate footprints from the 'Keuper' Sandstone are of Upper Scythian age, equivalent to those of the Solling Folge of the Upper Buntsandstein (i.e. so la—Kozur 1975, below Rötquartzit) according to Demathieu and Haubold (1972), the distinctive burrows of *Thalassinoides* cf. *suevicus* in the Waterstones are only known from strata of Anisian age in Germany (Upper Röt, so 2 or Wellenkalk, mu). Although to claim such precise dating based on trace fossils might be unwise, the above evidence agrees with the Scythian–Anisian age of the Cheshire Waterstones suggested by palynology (Warrington 1970*b*; Fisher 1972; Warrington *et al.* 1980).

SYSTEMATIC DESCRIPTIONS

All the invertebrate trace fossils recorded from the Waterstones are briefly described and compared with German type or figured material, since this is the first detailed study of an ichnofauna from the British Triassic. Where the trace fossils have been described previously (Ireland *et al.* 1978) only abbreviated synonymies, diagnosis, and brief remarks are given, although all the forms are illustrated on Plates 86–90 to justify the analysis and comparisons made. In accordance with common ichnological procedure (Häntzschel 1975; Crimes and Harper 1977) the ichnogenera are considered in alphabetical order rather than in any formal morphological or behavioural grouping. Specimens prefixed MGSF are in Special Collections, Geology Department, University of Manchester.

Ichnogenus ARENICOLITES Salter 1857
cf. *Arenicolites* sp.

Plate 86, fig. 3

1978 *Arenicolites* sp. Ireland *et al.*, p. 416, pl. 22, fig. 3.

Material. Endichnia: 3 specimens collected showing about 6 tube pairs. (Many isolate or paired burrows recorded in field—text-fig. 5, left).

Occurrence. These burrows are known only at Red Brow Quarry (locality 3) where they occur in at least 6 beds representing 2 lithofacies types (text-fig. 5, left).

Diagnosis. Vertical or slightly oblique paired burrows, circular in cross-section with mud-lined walls. Burrow diameters (6–12 mm) and spacing of tubes varies with lithology, being 70–80 mm apart in cross-bedded sandstone and 16–30 mm in thin-bedded rippled sandstones (Pl. 86, fig. 3). Base of burrows not observed.

Remarks. Despite the absence of undoubted basal U-bend, from the paired association, burrow morphology, depth, attitude, and lack of bedding disturbance, it is believed that these burrows belong to the ichnogenus *Arenicolites*. The same criteria and relative sparsity exclude them from *Skolithos*. The circular bedding plane expression of these burrows is similar to that of *A. kahlaensis* Kolesch (1922) from the Middle Buntsandstein and different from that with enlarged funnels of *A. franconicus* Trusheim (1934) from the Muschelkalk, although the ichnogeneric assignment of these forms is questionable (Fürsich 1974*a*, p. 8). The smaller form of this burrow is similar in size and morphology to topotype material of *A. sylvestris* Ortolam (1967) collected personally from the Röt sandstone of northern Schwartzwald of Germany.

Ichnogenus DIPLOCRATERION Torell 1870
Diplocraterion luniforme (Blanckenhorn) 1916

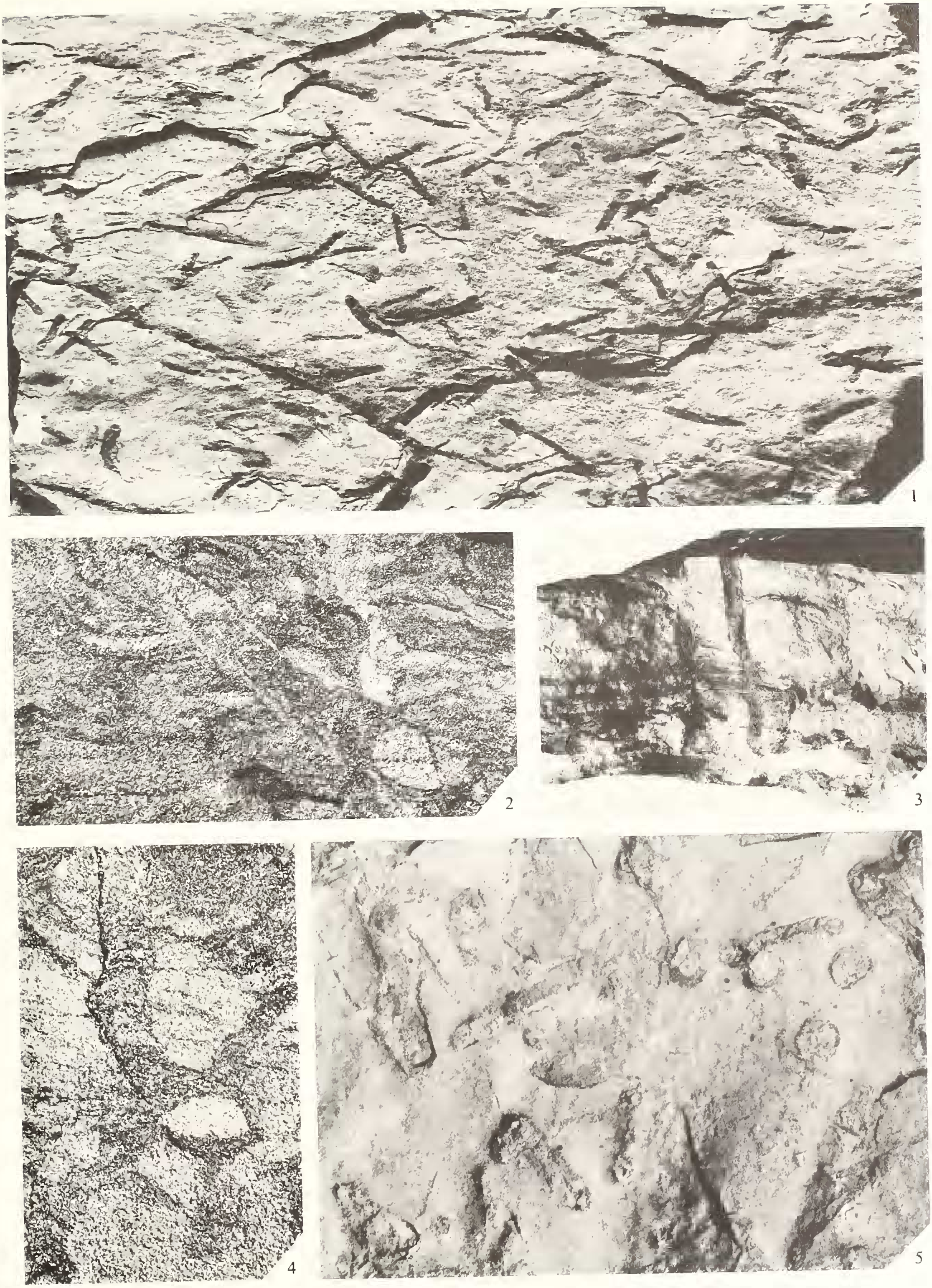
Plate 86, figs. 1, 2, 4, and 5

1916 *Arenicoloides luniformis* Blanckenhorn, pp. 36–40.
1922 *Arenicolites lunaeformis* (Blanckenhorn), Kolesch, pp. 344–356, figs. 2–6.
1922 *Arencolites zimmermanni*, Kolesch, pp. 356–362, figs. 7–13.
1923 *Arenicoloides luniformis*, Schindewolf, pp. 662–670, figs. 1–4.
1923 *Arenicoloides luniformis*, Sörgel, pp. 510–549, figs. 2–3, 6, pl. 19–20.
1925 *Corophioides luniformis*, Blanckenhorn, pp. 269–278.
1926 *Corophioides luniformis*, Richter, pp. 200–219, pl. 3.

EXPLANATION OF PLATE 86

Figs. 1, 2, 4, 5. *Diplocraterion luniforme* (Blanckenhorn). 1, MGSF 17, oblique view of shale bedding plane within fine red sandstone (lithofacies B) showing random oriented 'dumb-bell' burrows, some intersecting in a 'chicken's foot' pattern. Red Brow Quarry (locality 3), Waterstones. ×0·5. 2, MGSF 18, vertical cut surface of bioturbated sandstone (lithofacies A) showing oblique protrusive U-burrow (top left–bottom right). Locality and horizon as 1. ×1·5. 4, MGSF 18, expression as 2 but showing vertical protrusive U-burrow with compressed marginal tube. Locality and horizon as 1. ×1·8. 5, MGSF 22, bedding plane in ripple marked fine sandstone (lithofacies B) showing large 'dumb-bells' and vertical free tubes with concentric packed wall structure. Stretton (locality 4), Lower Keuper Marl. ×0·6.

Fig. 3, cf. *Arenicolites* sp., MGSF 20, parallel-bedded fine sandstone (lithofacies B) with paired vertical tubes with mud-lined walls but without intervening spreite. Red Brow Quarry (locality 3), Waterstones. ×0·5.



POLLARD, Triassic trace fossils

v1928*b* *Corophioides luniformis*, Schindewolf, pp. 40–41, fig. 12.
1932 *Corophioides luniformis*, Magdefrau, pp. 229–232, figs. 1–2.
1935 *Corophioides luniformis*, Abel, pp. 452–456, figs. 378–380.
1963 *Corophioides luniformis*, Seilacher, pp. 86–87, figs. 3–4.
v1967 *Corophioides luniformis*, Diederich, pp. 232–234, pl. 2, figs. 1–2.
1970 *Corophioides luniformis*, Osgood, pp. 315–316.
1973 *Diplocraterion luniforme*, Knox, pp. 142–143.
1974*a* *Diplocraterion parallelum* (in part), Fürisch, pp. 958–959, fig. 2.
1978 *Diplocraterion luniforme*, Ireland *et al.*, pp. 414–416, pl. 24, figs. 1–2.

(For a complete synonymy see *D. parallelum* Fürsich 1974*a*, p. 958).

Material. Endichnia, 8 specimens; hypichnia, 9 specimens.

Occurrence. Larger endichnial forms of *D. luniforme* are only known for the channel bar sandstones at locality 3, whilst the 'dumb-bell' expression also occurs abundantly here in ripple-marked, thin-bedded sandstones (text-fig. 5) and in similar lithologies at localities 4 and 8.

Diagnosis. Small to medium size, vertical to slightly oblique U-burrows with parallel or downwardly divergent marginal tubes, symmetrical or asymmetrical protrusive spreite and a distinctive luniform basal cross-section on bedding planes. The width of the U-burrow varies from 10 to 70 mm (mode 20–30 mm), the depth from 10 to 100 mm usually < 25 mm), and the marginal tube diameter is 2–3 mm, or very rarely 5–8 mm (see Table 2).

TABLE 2. Comparison of dimensions and frequency of *D. luniforme* from Buntsandstein of Germany and Waterstones and Lower Keuper Marl of Cheshire.

Formation and region or locality (see text-figs. 1 and 2)	Author (or specimen index and number of burrows)	U-burrow width mm (= mode)	U-burrow depth mm	Marginal tube diameter mm	Calculated number of burrows/m²
BUNTSANDSTEIN					
Schwarzwald	Brauhauser 1910	20–25	—	—	—
	Regelman 1919	20–30	*c.* 10	2–3	—
Hessen	Blanckenhorn 1916	20–25	*c.* 10	2–5	4000
	Schindewolf 1923	10–20	2·5–12	2–3*	5000–6000*
	Lohman 1960	*c.* 30	100	3–5	—
	Diederich 1967	7–25 (15)	—	2	3700*
Thuringia	Sörgel 1923	13–41	1–22		2000
	Kolesch 1921	10–50	4–130	2–3	—
	Magdefrau 1932	20–30	2–30	3	—
WATERSTONES					
locality 3	MGSF 17 (75)	10–45 (20–30)	15–40	2–3	1350
	MGSF 41 (30)	18–35 (20–30)	—	2–3	980
	MGSF 42 (25)	15–50 (*c.* 30)	—	3	800
	MGSF 43 (36)	20–45 (*c.* 30)	—	2–3	850
	MGSF 18 (10)	60–70	60–100	5	—
locality 8	MGSF 44 (25)	17–44 (20–30)	1–25	3–5	1900
	MGSF 45 (28)	10–45 (30)	2–5	2–3	*c.* 3000
L. KEUPER MARL					
locality 4	MGSF 22 (40)	20–65	30–50	2–8	950

* Personal observation and calculation.

Remarks. In terms of morphology, bedding-plane expression, and size, the U-burrows from Cheshire are identical to *Arenicoloides luniformis* Blanckenhorn from the Buntsandstein of Germany (See Table 2). As is shown in the synonymy, this ichnospecies subsequently has been assigned to the ichnogenera *Corophioides* and *Diplocraterion*. Several recent workers (i.e. Frey and Chowns 1972; Fürsich 1974*a*; Knox in Fürsich 1974*a*) have shown that specimens of *Diplocraterion* and *Corophioides* are intergradational and the ichnogenera, therefore, synonymous. However, not all workers have accepted this view (e.g. Hakes 1976; Baldwin 1977) and the name *Corophioides* is still extensively used by German workers for wide shallow U-shaped spreiten burrows, especially where these occur in 'dumb-bell' bedding-plane expression. Fürsich (1974*a*) considers that *D. luniforme* is synonymous with *D. parallelum*. Whilst it is apparent that these burrows are of *D. parallelum* type, as distinct from the other five ichnospecies of *Diplocraterion* he defined, it is considered that use of this name would obscure the close similarity of these distinctive British and German Triassic burrows. The shallow nature, distinctive luniform bedding-plane expression, restricted size range, and dominantly protrusive, somewhat irregular spreiten are characters which together make this a distinct ichnospecies, and hence the name *D. luniforme* is retained.

In the more intensely bioturbated beds containing *D. luniforme*, the endichnial expression shows that these protrusive U-burrows may become oblique (Pl. 86, fig. 2) or show marginal tube enlargement (Pl. 86, fig. 4), characters somewhat similar to the '*Glossifungites*' variant of *Rhizocorallium jenense* (Seilacher 1967; Gall 1971). Intersection of adjacent burrows on the bedding-plane expression (Pl. 86, figs. 1 and 5) to produce a 'chicken foot' (Huhnertreppe) trace occurs only occasionally in Cheshire specimens, as the bedding-plane frequency is only 800–3000/m^2 (Table 2). The preservation of these shallow U-burrows as epichnial lunate grooves is also the dominant mode of expression of *D. luniforme* in the Buntsandstein (Table 2, Sörgel 1923), although the frequency of burrows is higher there than in Cheshire (Table 2) and retrusive movement is known (Abel 1935; Seilacher 1963). Slight lateral movement of both U-bend and vertical tubes is present at some localities in Cheshire (e.g. locality 4, Pl. 86, fig. 5).

Toponomic analysis of *D. luniforme* ichnocoenoses from both Cheshire Waterstones (Ireland *et al.* 1978, p. 420) and German Buntsandstein suggests that these are dwelling burrows of communities of approximately equal age, suspension-feeding invertebrates, living under conditions of turbulence but without strong preferred current flow.

Ichnogenus ISOPODICHNUS Bornemann 1889

Isopodichnus sp.

Plate 87, figs. 1, 2

1978 cf. *Isopodichnus* Ireland *et al.*, pp. 418–419, pl. 22, fig. 3.

Material. Hypichnia: 2 specimens.

Occurrence. These rare traces have only been found at Red Brow Quarry, locality 3 on sole surfaces of lithofacies B sandstones (see Table 1, text-fig. 5 and Ireland *et al.*, Pl. 23).

Diagnosis. Small straight or curved double ribbon trails, preserved as hypichnia with median groove and transverse chevron-like striations. They are rarely associated with bilobate 'coffee bean' hypichnia of corresponding size. Width 6–8 mm, length > 20 mm for ribbon trace (*Cruziana* type), 13·5 mm and 17·0 mm for resting trace (*Rusophycus* type).

Remarks. The problem of synonymy or distinction of *Isopodichnus* from the ichnogenera *Cruziana* or *Rusophycus* has been discussed recently by several authors (Seilacher 1970; Birkenmaer and Bruton 1971; Bromley and Asgaard 1972, 1979; Trewin 1976; Hakes 1976). Whilst it must be admitted that these ichnogenera cannot always be distinguished on the basis of morphology alone, the size, geological age, facies association, and nature of probable non-trilobite producers suggest that *Isopodichnus* should be retained as a valid ichnogenus (Seilacher 1978).

The total characters of these traces, their width, ribbon-shape traces, short resting traces, and appendage scratch marks suggests referral to specimens of *Isopodichnus* (Schinderwolf 1928*a*; Trewin 1976). However, the poor state of preservation of the traces makes ichnospecific assignment uncertain, although in terms of width and behavioural variation it is similar to *I. problematicus* from the German Trias (Lower Buntsandstein—Röt; Schindewolf 1928*a* and personal collecting 1979). The traces described here appear to have been made as epichnial grooves in mud-draped ripples, as there is no burrowing disturbance in the overlying (casting) sandstone and the deepest (terminal) resting traces are normal to the ripple crest strike direction, suggesting rheotaxis (see Pl. 87, fig. 2*a*, cf. Seilacher 1953; Bromley and Asgaard 1972).

Ichnogenus LINGULICHNUS Hakes 1976
Lingulichnus cf. *verticalis* Hakes

Plate 87, figs. 6–8, text-fig. 6

?1934 'Vertical burrows with funnels', Rucklin, pp. 93–96, fig. 3*c–d*.
?1970 'Oval vertical tubes', Chisholm, p. 30, pl. IV, figs. 3–6.
1971 cf. *Cylindricum* (Les terriers de lingules) Gall, p. 70, pl. 22, figs. 1–2.
1976 *Lingulichnus verticalis* Hakes, pp. 27–29, fig. 10, pl. 6; fig. 5, pl. 7; fig. 1*a–d*.
1976 *Lingulichnites amygdalinus* Szmuc, Osgood and Meinke, pp. 163–167, figs. 1–2.
v1978 cf. *Lingulichnites amygdalinus* Gall, *in* Emig, Gall, Pajaud and Plaziat 1978, pp. 591–598, fig. 13, pl. 2; figs. 1–6.

Material. Endichnia: 6 specimens.

Occurrence. These burrows are known only from lithofacies B (intertidal sandflat deposits) in the lower part of the Waterstones at Red Brow Quarry, locality 3. This horizon also contains *Diplocraterion*, *Arenicolites*, *Palaeophycus*, etc., although actual bedding-plane association with *Lingulichnus* has not been observed.

Diagnosis. Vertical to slightly inclined parallel-sided burrow with elliptical cross-section and concentrically packed wall lining.

Description. This burrow consists of isolated, straight or slightly curved sediment-filled tubes with parallel sides and elliptical cross-sections, in a vertical or near vertical attitude (Pl. 87, fig. 6; cf. Hakes 1976, fig. 10). The width of the elliptical cross-sections with rounded ends is 7–10 mm in longest dimension, 3–4 mm in shortest and the depth of the tubes is > 50 mm. The lower ends of the tubes taper slightly and are rounded (Pl. 87, fig. 6; cf. Hakes 1976, fig. 10 and pl. 1*b*, *c*). The walls of the tubes have a thin but layered red or green mud lining, smooth internally but with a rough exterior which is frequently slickensided. Moulds of the exterior of the tubes in the surrounding matrix show crude annular corrugations or transverse indentations (Pl. 87, figs. 7 and 8) suggesting

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EXPLANATION OF PLATE 87

Figs. 1, 2. *Isopodichnus* sp., hypichnia on ripple-marked surfaces of thin sandstones (lithofacies B). Red Brow Quarry (locality 3), Waterstones. 1, MGSF 21, curved *Cruziana*-like ribbon trace deepening into a ripple trough. ×1. 2, MGSF 23 poorly preserved traces consisting of: (*a*)—crudely bilobate resting traces; (*b*, *c*)—ribbon trails; (*d*, *e*)—appendage scratch marks. The complete trail appears to cross the ripple marked surface in a zigzag manner. ×1.

Figs. 3–5. Striated oblique burrows. 3, MGSF 24, sand-filled burrow cast preserved on ripple-marked bedding plane. Mud-flake moulds impressed into the ripples are visible. Red Brow Quarry (locality 3), Waterstones. ×0·6. 4, MGSF 24 enlarged view showing tongue-shaped outline of the burrow and scratch moulding. ×1·5. 5, MGSF 25 another burrow preserved as positive hypichnia on base of ripple-marked sandstone but showing only poorly preserved scratch-marks. Locality and horizon as 3, 4. ×2.

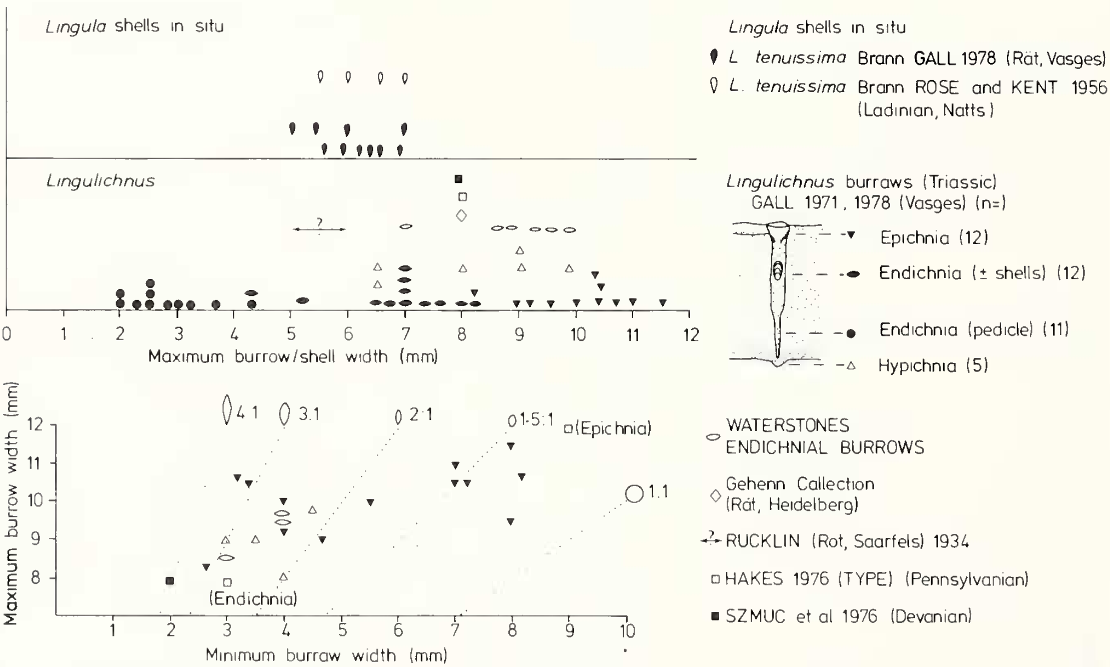
Figs. 6–8. *Lingulichnus verticalis* Hakes on broken surfaces of fine sandstones (lithofacies B). Red Brow Quarry (locality 3) Waterstones. 6, MGSF 26, vertical burrow with elliptical cross-section, tapering but rounded lower end and layered muddy wall lining. ×1. 7, MGSF 27, external mould of burrow wall showing crude transverse corrugate or annulate expression. ×1. 8, MGSF 28, expression as fig. 7 but with vertical striation on wall mould in upper part of burrow suggesting 'up and down' movement of occupant. ×1.

POLLARD, Triassic trace fossils

concentric packing of a mud lining into the tube wall. The infilling of the tubes is a structureless, muddy fine sandstone, siltstone, or mudstone. These burrows are preserved as positive or negative endichnia in red or grey-green fine sandstone. Epichnial bedding plane expression of these burrows has not been observed (cf. Gall *in* Emig et al. 1978, fig. 13, pl. 2; fig. 1).

Remarks. Two slightly different trace fossils have recently been interpreted as dwelling burrows of lingulid brachiopods, namely *Lingulichnus* Hakes (1976) and *Lingulichnites* Szmuc, Osgood and Meinke (1976), although neither contained lingulid shells *in situ*. *Lingulichnus verticalis* Hakes are vertical burrows with elliptical cross-section and concentrically packed wall lining, while *Lingulichnites amygdalinus* Szmuc *et al.* consists of tongue-shaped vertical burrows with elliptical cross-section and frequently a lower (pedicle) burrow with smaller diameter and nearly circular cross-section. As these burrows are very similar in size, form, and interpretation, Osgood has compared type material, confirmed synonymity, and given priority to *Lingulichnus* (Szmuc *et al.* 1977).

The burrows described here are very similar to *Lingulichnus verticalis* in terms of vertical attitude, elliptical cross-section, size dimensions (text-fig. 6), tapering but rounded lower end, and layered wall lining. No evidence of a pedicle tube below the main burrow, as seen in *Lingulichnites amygdalinus*, is preserved in the Waterstones forms, although it is present in burrows containing *Lingula tenuissima* in the *Voltzia* Sandstone (Röt) of the Vosges (Gall in Emig *et al.* 1978). The Waterstones and *Voltzia* Sandstone burrows have been compared (see text-fig. 6) and are considered to be toponomic variations of the same burrows. The burrows in the *Voltzia* Sandstone are preserved as endichnia without mud-layered wall lining (Gall, op. cit., p. 596, fig. 13, pl. 2), with elliptical to circular-shaped epichnial expression, probably caused by slight subsidence around the mouth of the burrow (see text-fig. 6, lower part), and rarely ovoid hypichnial expression. The positive hypichnial expression may result either from the position of anchorage of the pedicle in the sediment (Gall op. cit.), or from the



TEXT-FIG. 6. Comparison of width parameters of *Lingula* shells and *Lingulichnus* burrows from Triassic sediments of Britain, France, and Germany. Details of Palaeozoic type or syntype specimens of *Lingulichnus* are also included.

former position of the burrow prior to retrusive movement, as the size and shape seems closer to those of the major dwelling burrow than to those of the pedicle tube (see text-fig. 6). The Waterstones burrows are similar in depth to those from the *Voltzia* Sandstone, although greater in maximum width presumably on account of the concentrically packed wall lining enlarging the burrows laterally (see Hakes 1976, p. 28). The maximum width and maximum/minimum width ratios of the Waterstones burrows overlap with those of the epichnial and hypichnial expressions of the *Voltzia* Sandstone specimens (text-fig. 6).

These sparsely scattered lingulid burrows from the Waterstones were preserved by passive infilling, perhaps following vacation by their occupants at death (Craig 1952), in contrast to the *in situ* preservation of the abundant (5000/m_2) lingulid infauna of the *Voltzia* Sandstone, which were probably killed by prolonged emergence of their substrate (Gall, in Emig *et al.* 1978).

Although lingulid burrows have not been described previously from the Triassic of Britain, *Lingula tenuissima* in life position (identical to shells from *Voltzia* Sandstone—text-fig. 6) has been recorded from siltstones and muddy sandstones of the Waterstones (Carlton Formation, Ladinian) of Nottinghamshire (Rose and Kent 1955). *Lingula* shells have also been recorded from boreholes in 'Keuper' Sandstone of Oxfordshire (Warrington 1976) and Keuper Marl in Gloucestershire (Jeans 1978, p. 556).

Ichnogenus PALAEOPHYCUS Hall 1847
Palaeophycus triadica (Fliche) 1906

Plate 88, figs. 1–5

non 1852 *Palaeophycus striatus* Hall, p. 22, pl. 10, fig. 1.
non 1862 *Chondites triadicus* Geinitz, p. 132, pl. 24, fig. 4.
1906 *Spongillopsis triadica* Fliche, pp. 33–34, pl. 2, fig. 2.
?1961 *Palaeophycus* sp. large form. Linck, pp. 13–15, pl. 2, fig. 2.
1978 ?*Scoyenia triadica* Ireland *et al.*, pp. 416–418, pl. 22, fig. 1.

Material. Hypichnia: 7 discrete specimens and 5 walling slabs (uncollected).

Occurrence. This distinctive type of burrow is common at most localities where rippled and mudcracked bedding-plane surfaces are preserved (Table 1).

Diagnosis. Horizontal, straight or slightly curved fusiform burrows or cylindrical shallow U-burrows, with structureless infill and longitudinal anastomosing striate surface sculpture. Burrow diameter 1–10 mm (mode 6–8 mm), length 5–10 mm (mode *c.* 25 mm), and depth up to 15 mm. Burrows unbranched but may lie parallel or intersect at angles up to 90° (Pl. 88, fig. 1) and form networks which superficially resemble small thalassinoid burrow systems (Pl. 88, figs. 4 and 5). Frequently burrows are associated with sand-filled mudcracks (Pl. 88, figs. 1 and 2) or rarely vertical burrows of similar diameter (Pl. 88, fig. 1, *top left*). Sculpture of longitudinal ridges 5–10 in number, each up to 0·1 mm wide and 0·5 mm apart on widest burrows (Pl. 88, fig. 3) or of fine anastomosing striae on smaller burrows (Pl. 88, fig. 2).

Remarks. On account of the horizontal attitude, coherent sculptured wall, structureless sand infill, and inferred locomotory origin, this burrow appears to be assignable to the ichnogenus *Palaeophycus*. This is a broadly defined ichnogenus recorded from a variety of environmental situations and badly in need of taxonomic restudy (Osgood 1970; Frey and Chowns 1972; Hakes 1976).

This burrow form bears some resemblance to *Palaeophycus striatum* Hall (Osgood 1970, pl. 76, figs. 6, 7) in surface sculpture which may continue beyond the burrow on the interface and in hypichnial association with small stuffed burrows or resting traces, but differs in fusiform outline and lack of the stronger median ridge to the sculpture. The wall sculpture is close to that of ichnospecies of *Trichophycus* Miller, but the lack of spreiten and structureless burrow fill excludes it from that ichnogenus (Frey and Chowns 1972, pp. 29–30). The lack of recurved palmate branching separates this form from *Chondrites triadicus* Geinitz, but in burrow form, diameter, and surface sculpture it appears to be identical to *Spongillopsis triadica* Fliche (1906) from Muschelkalk of Lorraine, France. Häntzschel (1975, pp. W89, 101) suggests that *S. triadica* Fliche should probably be reassigned to *Rhizocorallium* Zenker along with the more recurved, possibly spreiten form, *S. recurva* Fliche. The form described here certainly does not belong to *Rhizocorallium*. The straight form of this burrow is similar in length, width, and bedding-plane expression to *Planolites rugulosus* Reineck, but it lacks the segmentally restricted ornament and meniscus packed internal fill of that ichnospecies. *P. rugulosus* Reineck is now generally regarded as full relief hypichnial expression of *Scoyenia gracilis* White (Seilacher 1963; Müller 1969; Häntzschel 1975; Bromley and Asgaard 1979). Although burrows of this general type and size have been figured by several authors from German Trias (e.g. Linck 1961) as *Palaeophycus* sp., only the ichnospecies *S. triadica* Fliche closely agrees with the burrow form described here.

This trace fossil is interpreted as a surface burrow groove, or near surface burrow made by a bristled or limbed invertebrate during locomotion. The vertical sinuosity, double or multiple galleries, and cross-cutting intersections suggest that the organisms responsible exhibited both shallow-burrowing and surface-crawling locomotion behaviour. The burrows were made on or in a distinct mud layer, either in ripple troughs or on mudcracked surfaces, probably under very shallow water at a time just predating the drying out of the sediment, since they frequently are cut by, or terminate against, mudcracks. Some burrows appear to have been formed in association with sandfilled mudcracks following resubmergence. The preservation situations indicated resemble very closely those of the *Scoyenia* ichnocoenosis in the Upper Triassic of Greenland (Bromley and Asgaard 1979, p. 78).

The badly weathered *P. triadica?* burrow systems described from localities 5 and 6 (Pl. 88, figs. 4 and 5) could represent intense burrowing of a thicker mud or muddy silt layer beneath water by an invertebrate community with a high population density. This would explain the interweaving and intersection of the burrows and the unusual apparent branching pattern, which would represent the producer's attempt to avoid previous burrows. Such complex interwoven burrow systems might indicate, at least in part, a feeding or feeding-dwelling function.

Ichnogenus PHYCODES Richter 1850
Phycodes curvipalmatum ichnosp. nov.

Plate 89, figs. 1–3, text-fig. 7

cf. 1852 *Buthotrephis palmata* Hall, p. 20, pl. 6, fig. 1; pl. 7, figs. 1*a*, *b*.
cf. 1862 *Chondrites triadicus* Geinitz, p. 132; pl. 24, fig. 1.
1937 *Palaeophycus* sp., Kuhn, pp. 371–372, fig. 5.
1961 *Palaeophycus* (small form) Linck, p. 65, pl. 1, fig. 3.

Derivation of name. From Latin *curvus*, curved, *palmatus*, palm of hand, referring to branching pattern.

EXPLANATION OF PLATE 88

Figs. 1–5. *Palaeophycus triadica* (Fliche). 1, MGSF 29, ripple-marked basal surface of fine sandstone (lithofacies B) showing short fusiform striated burrows in association with mudcracks. Red Brow Quarry (locality 3), Waterstones. ×1. 2, MGSF 30, mudcracked basal surface of thin sandstone with very shallow U-form (fusiform) burrows showing longitudinally striate surface sculpture. Stretton (locality 4), Lower Keuper Marl. ×1·2. 3, MGSF 29, enlarged view of burrow in lower left of fig. 1, showing parallel longitudinal striate sculpture. ×2·5. 4, (not collected), bottom surface of a sandstone bed (walling slab) showing a burrow system formed by intersecting and apparently branching burrows at slightly different levels. Boothsbank (locality 5), Waterstones? ×0·6. 5, (not collected), bottom surface of sandstone (walling slab in vertical position) showing complex burrow network adjacent to low symmetrical ripple marks. Locality and horizon as 4. ×0·1 (scale 0·5 m).

POLLARD, Triassic trace fossil *Palaeophycus*

Holotype. Special collections, Geology Department, University of Manchester, MGSF 32.

Paratypes. MGSF 31 and MGSF 33.

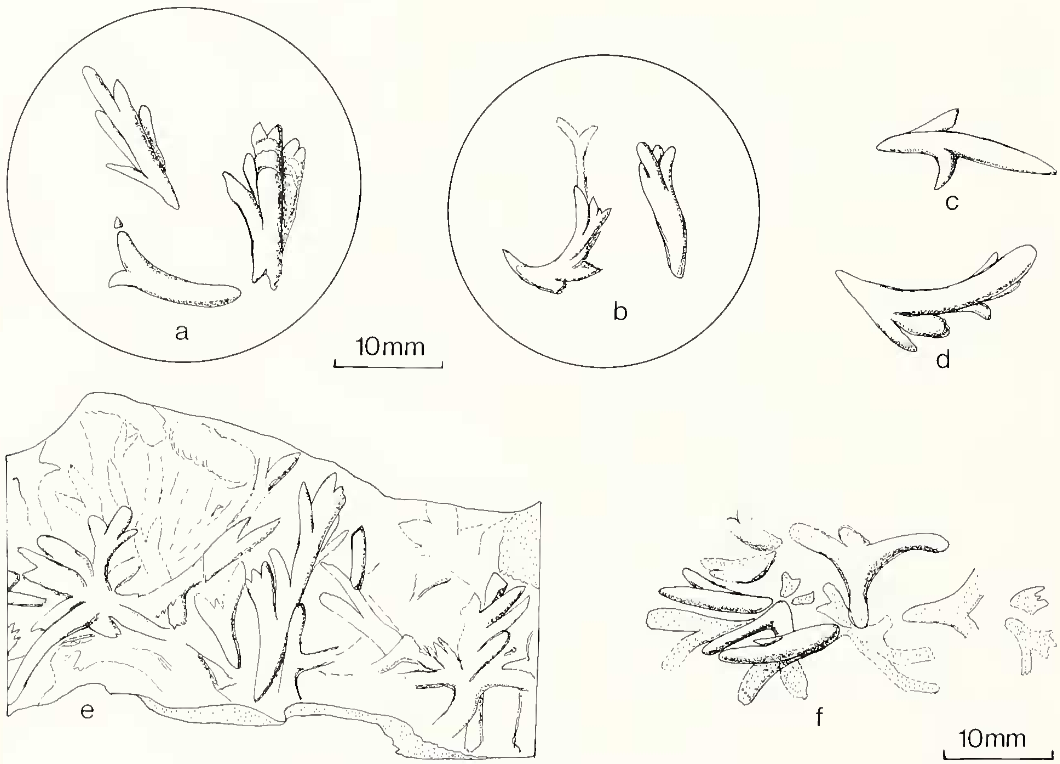
Type localities. Holotype, Styal, Cheshire; Paratypes, M56 cutting, Sharston, Cheshire.

Horizon. Waterstones Formation (= Tarporley Siltstone Formation) Scythian–Anisian stag Trassi

Occurrence. These burrows are common in the upper part of the Waterstones at Agden Hall (locality 5), Sharston and Styal (localities 8 and 9) but they appear rarely in the Upper Waterstones at Preston on Hill near Red Brow (locality 3) and in the Lower Keuper Marl at Stretton (locality 4) (see Table 1).

Diagnosis. Horizontal, cylindrical, or compressed burrows, 1–2 mm in diameter which are curved and branch either dichotomously or palmately, like the fingers of a hand.

Description. This trace fossil occurs in two distinct situations, either as isolate dichotomous or palmate burrows, or as complex interwoven burrow networks, both preserved as hypichnia (Pl. 89, figs. 1–3, text-fig. 7). The simplest burrow form is a curved 'Y' shape up to 20 mm in length and 1–2 mm in burrow diameter (Pl. 89, fig. 5, text-fig. 7*a*, *c*, *f*) but more usually these isolate burrows have short closely appressed branches in a palmate or frond-like arrangement (Pl. 89, figs. 2 and 3, text-fig. 7*a*, *b*, *d*). The burrow networks occur on the base of thin sandstone layers, are only 2–3 mm in depth and are composed of interwoven dichotomous or palmate branches at slightly different levels which sometimes appear to radiate from centres like the roots of a tree (Pl. 89, figs. 1–2, text-fig. 7*e*). Interbranch angle is 10–30° but it can reach 90° where the branch is strongly recurved from the main burrow (Pl. 89, fig. 3, text-fig. 7*f*). Burrow diameter rarely exceeds 2 mm and branches are usually < 10 mm in



TEXT-FIG. 7. *Phycodes curvipalmatum* sp. nov. *a–e* burrows (hypichnia) from holotype slab MGSF 32 (Pl. 89, fig. 2) showing associated (encircled *a*, *b*) and isolated, (*c*. *d*) recurved and palmate forms, and interwoven burrow network (*e*); *f*—paratype MGSF 23 (Pl. 89, fig. 3) (hypichnia) showing radiate 1st order dichotomous branches which overlap and curve upwards.

length. Burrow infill is a structureless mica-poor fine sandstone and burrow walls appear to be smooth and unlined.

Isolated examples of this burrow commonly occur in association with small stuffed burrows or resting traces (see Pl. 89, figs. 5 and 6) but such traces are very rarely associated with burrow networks.

Remarks. The branching pattern resembles that of *Phycodes* [*Buthotrephis*] *palmata* Hall, although these branches are more curved, shorter, and have a considerably smaller diameter and are therefore believed to constitute a new ichnospecies. This conclusion is supported by the difference of these burrows from larger radiate dichotomous burrows, virtually identical with syntypes of *P. palmata* figured by Osgood (1970, pl. 67, fig. 7), from the Middle Buntsandstein of the Spessart area, preserved in the Hessen Landesmuseum, Darmstadt (Backhaus 1967; pl. 2, fig. 4). These burrows lack the distinct curvature and annulation of the branches characteristic of cf. *P. pedum* Seilacher, a form which is known from Middle Buntsandstein of the Heidelberg area (Seilacher 1963, fig. 5). However, burrows of a generally similar recurved triad or palmate branching type, probably referrable to this ichnospecies, are known from several levels in Germany, namely: Buntsandstein associated with marine bivalves (Geinitz 1862); Solling Group, Upper Buntsandstein (Backhaus 1967, pl. 2, fig. 3); Lettenkeuper, *Acrodus* Bank (Kuhn 1937, fig. 5); Kieselsandstein (km 3) (author's collection MGSF 50); and Stubensandstein (km 4) (Linck 1961, pl. 1, fig. 3 and Stuttgart Museum Naturkunde specimen 24453).

The intimate association of the simplest forms of these burrows with ovoid-elongate stuffed burrows described below (Pl. 89, figs. 5 and 6) suggests that these two trace fossils may represent different behaviour patterns of the same organism. However, the complex interwoven burrow networks (Pl. 89, figs. 1 and 2, text-fig. 7*e*) clearly represent fodinichnial burrowing of a thin mud layer at shallow depth below sand, but give no clue as to the affinities of the organism responsible.

Ichnogenus PLANOLITES Nicholson 1873
Planolites sp.

1978 *Planolites* sp. (cf. *P. montanus* Richter type) Ireland *et al.*, p. 418.

Material. 10 specimens from 4 localities (see Table 1).

Occurrence. These burrows are known from the base of both channel bar sandstones (e.g. locality 2) and rippled thin-bedded sandstones (e.g. locality 2) and rippled thin-bedded sandstones and siltstones (localities 3, 6, and 7).

Diagnosis. Short compressed sand-filled burrows of variable shape occur on shale bedding planes in the Waterstones in both epichnial and hypichnial preservation. Some burrows are straight, others are gently sinuous, all are unbranched, although they may occur in groups. Burrow diameter varies from 5 to 10 mm and length varies from 10 to 30 mm. No distinctive texture is preserved in the burrow fill.

Remarks. This heterogenous group of burrows appears to be referable to *Planolites.* Some of these burrows may represent poorly preserved specimens of the more distinctive burrow types described above while the so-called 'worm castings' and 'vermiform marks' of previous authors (Ireland *et al.* 1978, p. 401) are included here. Similar variable, somewhat indeterminate burrows have been illustrated or recorded from various horizons from L. Buntsandstein (e.g. Backhaus 1967, pl. 2, fig. 4) to Röt (= *Voltzia* Sandstein—Gall 1971, pl. 27, fig. 4; Gehenn Collection, Heidelberg), in the German Triassic basin.

Small stuffed burrows or resting traces

Plate 89, figs. 4–7

?1928 Casts of young *Apudites* sp., Sörgel, pl. 1, fig. 6; pl. 4, fig. 2.
?1949 Problematicum, Linck, p. 70, pl. 8, fig. 4.
non 1953 *Sagittichnus lincki* Seilacher, p. 116, pl. 13, figs. 1 and 2.
?1963 cf. *Phycodes pedum* Seilacher, fig. 5.
1965 Problematica, Hoppe, p. 297, pl. 6, fig. 2.
1976 Small stuffed burrows, Trewin, p. 35, fig. 4F.
1979 Small stuffed burrows, Bromley and Asgaard, p. 53, fig. 6*c*.

Material. Hypichnia: 10 specimens.

Occurrence. In upper part of the Waterstones at Red Brow and Preston on Hill (locality 3), Agden Hall (locality 5), and Sharston (locality 8) and in Lower Keuper Marl at Stretton (locality 4).

Diagnosis. Spheroidal, sub-ovate, heart-shaped, or elongate hypichnia often with one end more deeply impressed than the other, 2–5 mm in length, 1–3 mm in width. (In well-preserved specimens a shallow median groove may be seen in the broader and deeper end.)

Description. Small rounded to elongate hypichnia occur on the basal surface of thin ripple marked sandstones (Pl. 89, figs. 4–7). The apparent shape is quite variable, depending on the degree of weathering of the trace and the grain size of the casting medium, as well as on behavioural variation of the producer. The commonest shape is rounded or irregularly subovate, more rarely heart-shaped or elongate with a shallow median groove. The longest dimension varies from 2 to 5 mm, width from 1 to 3 mm, and depth about 2 mm. These traces may be doubled or arranged in linear or curved series, like a string of beads, up to 13 mm in length. Doubled or multiple traces may pass into curved or branching burrow casts which closely resemble *P. curvipalmatum* described above (Pl. 89, figs. 5, 6). Several traces are of a bilobate or minute 'coffee bean' form (Pl. 89, figs. 4 and 6) resembling a very small form of *Isopodichnus* (i.e. *I. stromnessi* Trewin).

The traces are most deeply impressed in the mud drape on flanks or troughs of symmetrical ripples where orientation of the longest dimension is usually random, although one slab from Stretton (locality 4) shows strong preferred orientation parallel to palaeocurrent direction, indicated by primary current lineation and an adjacent sole surface. These burrows are often associated with *P. curvipalmatum* and more rarely with small forms of *P. triadica* about 2 mm in diameter. Shallow depressions in the mud drape on ripple marks on the upper surface of

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EXPLANATION OF PLATE 89

Figs. 1–3. *Phycodes curvipalmatum* ichnosp. nov. 1, MGSF 31, bottom surface of a thin sandstone with a 5-mm thick layer of interwoven burrows showing dichotomous and palmate horizontal branching occasionally radiating from centres like tree roots (centre right and lower right). Sharston (locality 8), Waterstones. ×1. 2, MGSF 32, holotype, bottom surface of thin ripple-marked sandstone, showing a lower surface with shallow symmetrical ripples, a large mudcrack and isolate small curved palmate burrows, and a higher surface (upper left and upper right) with interwoven branching burrows. (See also text-fig. 7*a–e*.) Styal (locality 9), Waterstones. ×0·45. 3, MGSF 33, bottom surface of 15-mm thick sandstone bed showing small dichotomous and palmate branching burrows, some strongly recurved, all associated with halite pseudomorphs. (See also text-fig. 7*f*.) Locality and horizon as 1. ×1·6.

Figs. 4–7. Small stuffed burrows or resting traces. 4, MGSF 35, bottom surface of fine red sandstone with adhering shale showing ovate, triangular, or rarely 'bilobite' traces in isolate, grouped or en-echelon arrangements. Agden Hall (locality 6), Waterstones. ×1. 5, MGSF 34, bottom surface of fine red sandstone showing randomly oriented single, double, or elongate burrows or resting traces associated with branched burrows (cf. *Phycodes*) of at least two size classes. Locality and horizon as 4. ×0·8. 6, MGSF 36, bottom surface of sandstone with shale layer and a wide variety of ovate, elongate, repeated, and even curved ploughing traces, all in random orientation. Some elongate traces (centre) show fine median groove. Locality and horizon as 4. ×1. 7, MGSF 37, bottom surface of sandstone with spheroidal-triangular hypichnia informally described as 'pimple marks' (see text). Red Brow Quarry (locality 3), Waterstones. ×1·5.

POLLARD, Triassic trace fossils

sandstone beds, informally termed 'dimple marks' when similar in outline, dimensions, and distribution to this trace, may be its epichnial expression. However, some such marks are certainly of inorganic origin, produced by imprints of halite crystals or mud pellets.

Remarks. The morphology of these small burrows is so variable that they defy assignment to an ichnogenus but, as they show close similarity to burrows illustrated by Trewin (1976) and Bromley and Asgaard (1979) as 'small stuffed burrows', this name is used here.

Problematic trace fossils of this general form have been described from both the Buntsandstein and the Schilfsandstein of the German Trias (Sörgel 1928; Linck 1949; Seilacher 1953, 1963; Hoppe 1965). The triangular or heart-shaped outline of some of these burrows from Cheshire at first sight suggests similarity to the controversial structure *Sagittichnus lincki* Seilacher. However, comparison of these burrows with type material of *S. lincki* (Tübingen Ic 1009/35 and Stuttgart 22013) shows that this is not so, as the Cheshire specimens lack the keeled arrowhead shape, deepest at the pointed end, and the uniform preferred orientation of this 'ichnospecies'. *Sagittichnus* has recently been rejected as a trace fossil (Clemmensen 1978, p. 1122; Bromley and Asgaard 1979, p. 72) in favour of interpretation as an inorganic prod mark, although the precise mode of origin of such a distinctive shaped structure has yet to be explained. Some of the best-preserved sub-ovate and heart-shaped traces appear very similar to hypichnia from the Buntsandstein, interpreted as sandstone body casts (more likely resting traces) of young *Apudites* or *Euestheria* (Sörgel 1928; Hoppe 1965).

These rather variable burrows are here interpreted as either resting traces, showing rare rheotaxis but frequent lateral movement in a series of halting stages, or shallow feeding burrows, both produced by small invertebrates, possibly crustaceans, on or in the floors of shallow temporary pools.

Striated oblique burrows

Plate 87, figs. 3-5

1979 'Striated oblique burrows', Bromley and Asgaard, p. 51, figs. 7, 8.

Material. Hypichnia: 2 specimens (MGSF 24 and MGSF 25).

Occurrence. This rare form is only known from intertidal sandflat deposits at Red Brow Quarry, locality 3. Although not found in actual association with other trace fossils it appears that traces such as *Palaeophycus triadica*, *Planolites*, *Isopodichnus*, and *Chirotherium* are more likely bedding-plane associates than the endichnial burrows *Diplocraterion*, *Arenicolites*, and *Lingulichnus* also found in this lithofacies (text-figs. 2 and 5).

Diagnosis. Small, horizontal, or slightly oblique, tongue-shaped pouch burrow with finely ridged or criss-cross striated wall sculpture. Preserved as positive hypichnia on mudcracked bedding plane surfaces.

Description. This new burrow is known from two specimens preserved as full relief hypichnia excavated in mud drape within ripple troughs (Pl. 87, figs. 3). One specimen MGSF 24 (Pl. 87, figs. 3 and 4) appears to cut across a fine sand-filled mudcrack. In shape this burrow resembles a tongue or an infilled parallel-sided pouch, which is inclined at about 10° to the horizontal and is slightly compressed and convex downwards (Pl. 87, figs. 4 and 5). The distal rounded terminations of the burrows are almost horizontal while the proximal ends, which may not be completely preserved, appear to curve obliquely upwards into the overlying casting bed. Dimensions are respectively: specimen MGSF 24—length 39 mm, median width 14·5 mm, and depth 3 mm; specimen MGSF 25—length 25 mm, median width 11 mm, and depth 4·4 mm. The burrows are filled with a structureless red sandstone. The outer surfaces of the burrow casts are covered with prominent fine ridges or coarse striae (scratch-marks) which have a longitudinal arrangement around the rim of the burrow but a curved diagonal or transverse arrangement on the top and bottom median surfaces (Pl. 87, figs. 4 and 5). These scratch-mark casts on the median surfaces are about 0·2–0·5 mm in width and up to 5 mm in length, and commonly appear to branch or intersect one another in a faintly criss-cross pattern.

Remarks. Bromley and Asgaard (1979) have recently described burrows, very similar in size, shape, sculpture, and attitude to those described here as 'striated oblique burrows' from the Ørsted Dal Member of the Triassic Fleming Fjord Formation of east Greenland. They interpret these burrows, which occur as semi-relief hypichnia on mudcracked bedding planes, as probable insect domichnia formed in a terrestrial environment.

The shape and scratch-mark pattern of the Waterstones specimens suggests that, like the Greenland burrows, they were excavated protrusively as oblique to horizontal pouches (Bromley and Asgaard, op. cit., fig. 8) in stiffening (drying out) mud but within the troughs of wave-formed ripples. However, the open burrows were passively filled with fine sand and preserved as full relief hypichnia attached to the overlying ripple cross-laminated sandstone bed but surrounded by shale. In the environmental situation of the Waterstones the arthropod producers of such burrows would be more likely to have been crustaceans than insects and indeed the scratch-mark patterns are very close to those shown by *Corophium* burrows in the mud of Recent tidal flats (Schäfer 1972, pl. 25*b*). No burrows of this type have yet been described from the German Triassic sequence.

Ichnogenus THALASSINOIDES Ehrenberg 1944
Thalassinoides cf. *suevicus* (Rieth) 1932

Plate 90, figs. 1–7, text-fig. 8

1910 *Spongeliomorpha* sp. Reis, pp. 256–259, pl. 11, figs. 12–22*c*.
1944 *Thalassinoides visurgiae* Fiege, pp. 416–421, 424, text-fig. 4.
1967 *Thalassinoides* cf. *suevicus* Kennedy, pp. 140–141, pl. 1, fig. 2.
1973 *Spongeliomorpha suevica* Fürsich; p. 730, text-fig. 6.
1978 *Thalassinoides* cf. *suevicus* Ireland *et al.*, p. 414, pl. 2, figs. *a–b*.

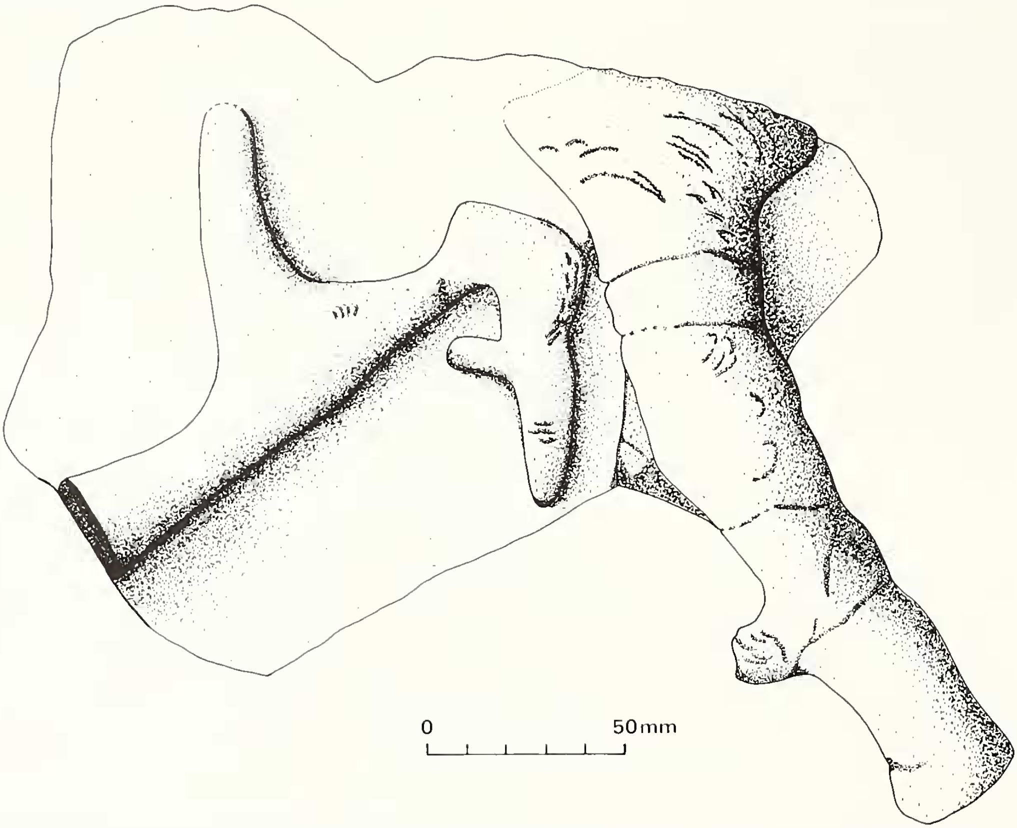
Material. This description is based on about 8 specimens from locality 3, 5 specimens from locality 2, and extensive field observations at localities 1, 2, and 3.

Occurrence. Fully developed burrow systems are only found on the base of the Red Brow Sandstone at locality 3 (Ireland *et al.* 1978, pl. 23). Isolated burrows or parts of small systems are present at other levels in this bed (text-fig. 5). Badly eroded semi-relief burrows of this ichnospecies occur at the base of lithofacies A or B sandstone units at localities 1 and 2 (see below).

Diagnosis. Mainly horizontal, cylindrical branching burrow systems, branching 'Y' and 'T' shaped, diameter of individual burrows more or less constant except at points of branching, burrow walls unlined or covered with scratch-marks. Burrow morphology and branching patterns are more varied than previously known in this ichnospecies, and are therefore described and analysed in more detail below.

Description. The form of *T.* cf. *suevicus* from Cheshire consists of cylindrical or vertically compressed burrow moulds which in their most complex pattern form a horizontal irregular 'maze' (Frey, Howard and Prior 1978, fig. 2) with polygonal (p), zigzag (z), or rarely antler-shaped branching elements at slightly different levels (Pl. 90, figs. 1 and 5). At localities 1 and 2 only isolated coarsely scratch-marked, antler-shaped branching elements associated with elbow-shaped 'turn arounds' are preserved. Interbranch angle varies from 35 to 130° but mainly between 70 and 130°. The burrow diameter varies from 10 to 65 mm without distinct size classes, although smaller short burrows 10–18 mm in diameter can originate abruptly from wider burrows (Pl. 90, fig. 5 and cf. text-fig. 8). The top of the burrows in the network has not been observed, but the base is often covered with coarse scratch-marks in a chevron or overlapping transverse arrangement (Pl. 90, fig. 5), whilst the sides of the burrow may show paired fine scratch-marks. One 18 mm diameter burrow mould (Pl. 90, figs. 3 and 4) observed cutting obliquely through a 0·3 m thick sandstone bed (Pl. 90, fig. 2) had a mamillated roof lining and a smooth floor in the manner of *Ophiomorpha* (Frey *et al.* 1978, fig. 5), presumably to resist collapse. The burrows are filled with either fine sandstone or sandstone with mudflakes, and are preserved as full relief or semi-relief hypichnia, usually associated with an erosion surface.

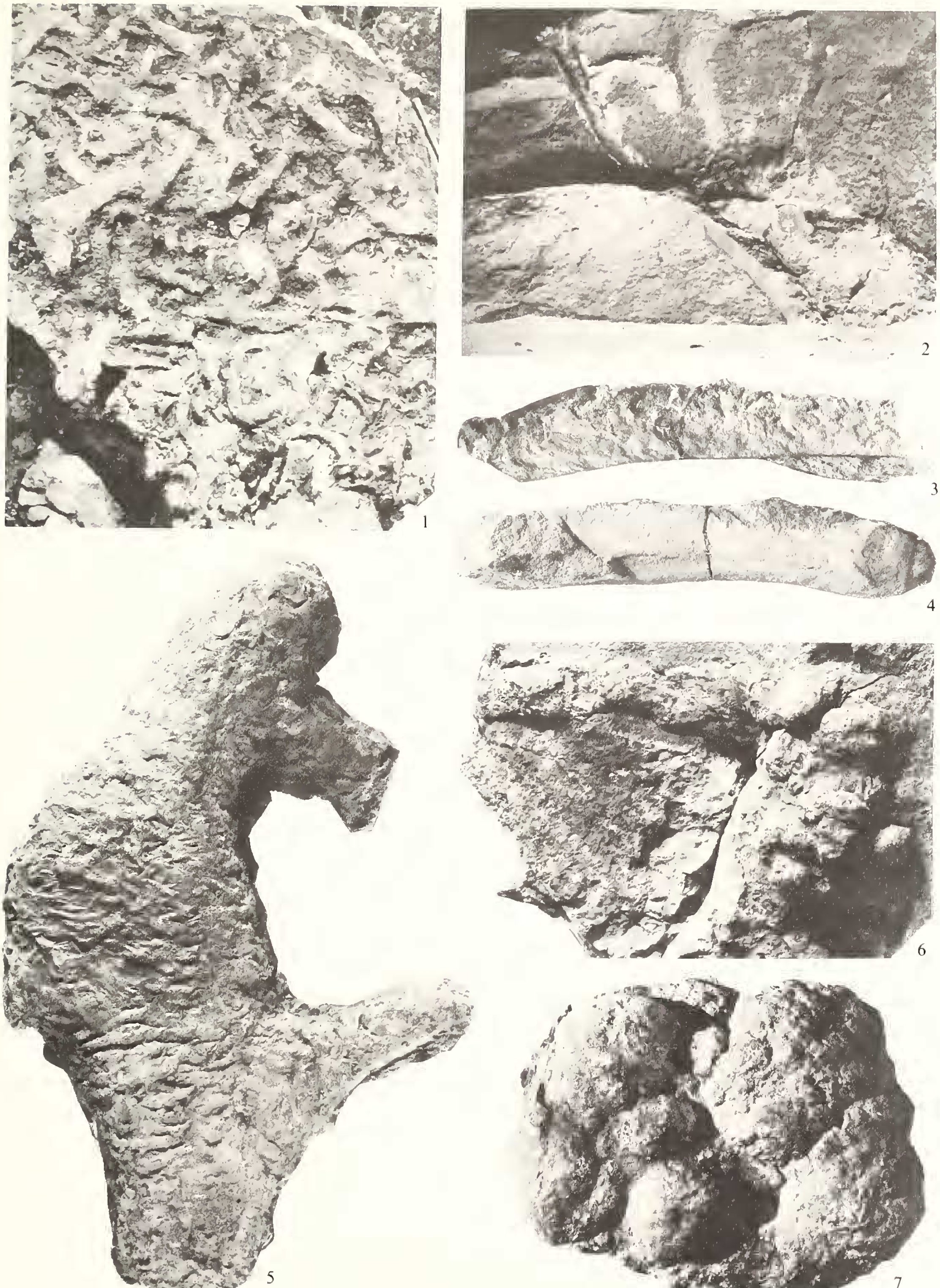
Short burrows 15–20 mm in diameter usually show one set of coarse chevron-shaped scratch-marks along the basal mid-line of the burrow (Pl. 90, fig. 5, lower right) whilst in other parts of the burrow system the burrows are inflated to node-like or flask-shaped enlargements with coarse basal scratching. Some of these enlargements resemble the ichnogenus *Pseudobilobites* (Kennedy 1967, pl. 7, fig. 3; pl. 9, fig. 4). Where the sole surface of the casting sandstone preserves only the deepest part of the original burrow system, positive hypichnia shaped like half cauliflowers are preserved attached basally or laterally to the burrows, or more frequently independent of them (Pl. 90, figs. 6 and 7). These burrow casts, which are usually about 30 × 50 mm in length and width and 25 mm in depth, but can be as large as 100 × 70 mm and 40 mm in depth, have distinctly nodose or mamillated lower surfaces (Pl. 90, figs. 6 and 7) and rarely showing fine scratch-marks. The distinctive shape and independent occurrence of many of these burrow casts suggests that they could be named as a distinct ichnogenus, but such a procedure has not been adopted here, as they are considered to be a specialized part of the thalassinoid burrow system (see discussion below).



TEXT-FIG. 8. *Thalassinoides* cf. *suevicus* from *Myophoria* Schichten, U. Röt (Anisian) at Helmstadt, Württemberg. The form of this burrow is similar to that from the Waterstones of Cheshire. (Drawn from a photograph of a specimen in the Gehenn Collection, Geological Institute, University of Heidelberg, Germany.)

EXPLANATION OF PLATE 90

Figs. 1–7. *Thalassinoides* cf. *suevicus* (Rieth) from medium sandstones (lithofacies A) Red Brow Quarry (locality 3), Waterstones. 1, (not collected), bottom surface of a sandstone block showing complex horizontal burrow system (boxwork) with Y-shaped, zigzag (z) and polygonal (p), branching elements preserved in full relief. ×0·08. 2, (not collected), broken vertical surface of parallel laminated sandstone cut by oblique burrow mould and cast (figs. 3, 4) with mamillated roof lining and smooth floor. ×0·4. 3, 4, MGSF 38, positive burrow cast removed from the sandstone bed in fig. 2, showing mamillated roof sculpture (3) and smooth floor with median groove (4). ×0·7. 5, MGSF 16, burrow cast as semi-relief hypichnia showing moulding of coarse and fine transverse scratch-marks and short 'blind' burrow (right) with chevron pattern of scratch moulds. ×0·6. 6, MGSF 39, sandstone cast of a tunnel which terminates in an irregular burrow cast resembling a deeply nodose cauliflower or bunch of grapes. ×0·35. 7, MGSF 40, hypichnial burrow cast resembling a cauliflower. ×0·85.



POLLARD, Triassic trace fossil *Thalassinoides*

Remarks. In terms of diameter, mode, and angle of branching, these burrows are closely comparable with *T. suevicus* from U. Jurassic (Fürsich 1974*b*) and U. Cretaceous (Kennedy 1967), although they differ apparently in the transverse pattern of scratch-marks and greater variety of burrow morphology. This transverse sculpture and the associated cauliflower-shaped burrow casts are both figured by Reis (1910, pl. 22, figs. 12, 13, and 22) as '*Spongeliomorpha*' from the German Muschelkalk; the form was subsequently redescribed by Fiege (1944) as *T. visurgiae*. Full to semi-relief hypichnial burrows of *T.* cf. *suevicus* from the *Myophoria* Schichten of the Upper Röt at Helmstadt (text-figs. 5 and 8) are virtually identical in size, burrow form, and branching pattern to specimens from the Cheshire Waterstones (compare text-fig. 8 and Pl. 90, figs. 1 and 5). The Helmstadt burrows are moulded by green sandstone below an erosion surface overlain by ripple cross-bedded and mudflake-bearing fine sandstone, very similar lithologically to the intertidal sandflat deposits at Red Brow Quarry (text-fig. 5).

Although *T. suevicus* burrow systems are generally interpreted as dwelling burrows of a glypheid crustacean (Fiege 1944; Selwood 1971; Fürsich 1974*b*) formed in a subtidal environment (*Cruziana* ichnofacies), certain distinctive features of these Triassic burrows suggest a closer analogy with Recent intertidal or supratidal decapod burrows. The shallow horizontal attitude, burrow size, and branching patterns associated with basally scratched burrow enlargements and specialized breeding or resting chamber moulds appear to be characters that these burrows share with the burrow systems of such Recent intertidal crustacea as *Callianassa* (Braithwaite and Talbot 1972, pl. 3A) or *Upogebia* (Bromley and Frey 1974, figs. 9–10). The burrow systems of *Alpheus heterochaelus* described by Bassan and Frey (1977, p. 59, pl. 2*d*, 3*a*) from the upper creek bank zone of the Georgia salt marshes have many features in common with the form of *T. suevicus* described here, and likewise were assigned by them to the *Glossifungites* ichnofacies.

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